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A COMPARATIVE STUDY OF THE DEVELOPMENT OF SOME ANTHRACNOSES.

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(WITH PLATES VII–XVIII)

INTRODUCTION.

THE investigations recorded in the following paper were undertaken (1) for the purpose of ascertaining by the growth characters developed in artificial cultures, the relationship of certain fungous diseases grouped under the common name of anthracnose, and (2) to determine, if possible, by a study of their life histories, the connection of these so-called imperfect fungi with perfect or ascigerous stages.

Following the established precedent I have included under this general term certain conidial forms belonging to the family Melanconiaceæ; and a few species of the closely related sphæropsidaceous genus Vermicularia, and Volutella belonging to the Tuberculariaceæ, which so closely approach the genus Colletotrichum in their structural characters and in the effect upon the host plant that diseases belonging to these genera have been referred to the anthracnoses,[1] have also been studied.

[1] The popular term anthracnose has no systematic value. The name first applied to the "bird's eye" fungus of the grape (*Sphaceloma ampelinum* De Bary, Bot. Zeit. **32**: 451. 1874) has since been applied to diseases having a similar external appearance and agreeing in general in microbotanical characters.

The greater number of diseases described as anthracnoses have fallen under the genera Glœosporium and Colletotrichum. These are characterized as fungi appearing at the time of fruiting in subcutaneous or subepidermal acervuli, which at maturity become partly erumpent. The conidia are borne upon basidia arising from a more or less definite basal stroma. At maturity the conidia issue upon the surface of the host in a conglutinated mass, usually of a roseate hue. The acervuli frequently occur upon the host in quite regular concentric circles. The characters of the genus Colletotrichum agree in the main with those of Glœosporium, with the exception of the presence of setæ in the former genus, which is not an absolute line of distinction, however, since Glœosporium develops occasional setæ, and the setæ in Colletotrichum sometimes become so reduced in number that the pustules cannot be distinguished from those of Glœosporium.

The large number of species of these genera, which closely resemble each other in structural characters, and the fact that the anthracnose of one host will adapt itself to others, indicate their close relationship, and suggest that many more species have been established than should be maintained. Moreover, species are often established, especially among the imperfect fungi, from characters which vary with the conditions of growth.

It is well known that these fungi, though parasitic, adapt themselves quite readily to saprophytic conditions, and may be grown in various nutrient media. In artificial cultures, distinct species present more or less marked growth characters, and it is with the aid of these characters that I have attempted to relate, or distinguish, the species of some of this group of fungi, since the characters peculiar to each are sufficiently constant and well marked to be of taxonomic value.

In studying the characters, the ordinary dilution culture method has been employed, and the colonies photographed from Petri dishes. The fungus is then transferred to tubes of sterilized nutrient media. Various media have been employed, but sterilized bean stems have proven the most satisfactory for gen-

eral purposes, as they are rich in nitrogenous matter and the fungus has a vigorous healthy growth upon a substratum of a consistency near that upon which they are accustomed to grow.

Of nearly all the species studied, the structural characters and relation to the host have received previous study from an economic standpoint; in such cases these points have been briefly mentioned. While germination of conidia has been observed in all species, a detailed account of those which agree quite closely would be tedious; it has, therefore, been usually omitted except in cases where some differences from the normal type have been observed.

Herbarium specimens, tube cultures, and microscopic mounts have been placed in the Botanical Department of Cornell University where the work has been conducted.

My acknowledgments are due to Professor George F. Atkinson at whose suggestion the work was undertaken and to whose ready advice and assistance I have been greatly indebted, and to Messrs. J. B. Ellis, S. M. Tracy, Byron D. Halsted, and others for their cheerful compliance to requests for fungi from their herbaria.

GLŒOSPORIUM FRUCTIGENUM Berk. (*figs. 1–4, 33–38, 83*).

This species, which has been so fully and carefully described by Miss Southworth,[2] and to which Mr. Alwood[3] has recently devoted considerable attention, is comparatively rare in the northern states. The material from which the disease was studied was obtained from apples in the northern markets and from quinces in an orchard at Ithaca. The presence of the fungus was indicated by the characteristic dark brown spots which spread rapidly in size and become somewhat sunken. The center of the spot becomes quite dark in color from the numerous black pustules which rupture the epidermis a few days after the spot has made its appearance. From some of the pustules the abundance of conidia presents a pale rose

[2] Jour. Myc. **6**: 164–173. 1891.

[3] Ag. Exp. Sta. Virginia, Bull. no. 40, May 1894.

color; at the margin of the spot the pustules are frequently arranged in concentric circles.

Sections of the fruiting bodies show the extreme variation marked by Miss Southworth. The developing stroma at the base of the pustule causes in some a depression in the tissue of the host, which is shrunken and brown for some distance down in the fruit. In others there is scarcely any depression; the base of the pustule is very narrow, and the basidia, which become septate with age and quite dark in color, spread gradually and extend a considerable distance above the host, giving the pustule in cross section a flabellate appearance. In the older pustules the disappearance of the basidia at the center was observed, and in addition to the ordinary conidia, on some of the elongated basidia were borne large oval or club-shaped bodies which become fuliginous, and are single-celled or once septate. They resemble the so-called secondary spores so frequently observed in artificial cultures. The conidia are hyaline, single-celled, elliptical, ovate or sometimes curved, varying considerably in size and shape.

In a dilution culture of meat-, or potato-agar, the conidia germinate readily within three or four hours. A germ tube is developed usually near the end of the conidium, which becomes coarsely granular and the contents begin slowly to pass into the tube. Two or three germ tubes frequently arise from the conidium. Sometimes the conidium upon germination becomes septate, but this is the exception under favorable conditions of growth. The fusion of the conidia mentioned by Mr. Alwood[4] is not peculiar to the species, but is frequently seen in other species, and is apparently due to a lack of nutrition, as it is most noticeable in water cultures or in agar-agar cultures when the growth is crowded, or when the nutritive material is exhausted.

Within two or three days after sowing is made, the small stellate colonies may be seen in the agar with the unaided eye. They are subcircular or elliptical, the center being marked by a slightly elevated, more compact growth of mycelium, elongated

[4] Loc. cit., 67.

and radiating in two to five directions. Upon this growth the first and most abundant development of conidia takes place, which gives it a flesh color; beyond this the growth is nearly uniform. The colony is almost colorless at first, later assuming a delicate flesh color with the pigment developed in connection with production of conidia. The conidia are formed acrogenously on the branches of the mycelium; as the successive ones are formed they push the older ones aside, where they may be seen lying in evenly arranged rows or piled up in little heaps. Becoming more numerously developed in some places, they form light pink acervuli quite evenly distributed over the colony.

On bean stems the fungus develops a dense white or grayish mycelium, which extends over the stems and the surface of the infusion in a flocculent weft. About three days after transferring, blackened fruiting sori make their appearance upon the stems; from these issue the pink masses of conidia, varying in color under different conditions; in parallel cultures the pigment had a deeper tint on infusion of apple than on bean stems. With age there is developed an abundant stroma, spreading over the stems and underlying the younger flocculent mycelium. The mycelium forming the stroma becomes coarse, irregular, and dark colored.

In old plate cultures the protoplasm of the mycelium has been seen to break up into elliptical spore-like bodies arranged somewhat diagonally in the cells or placed end to end. The dark, club-shaped bodies may be lacking in the entire life cycle of this species, but conidia sown in a hanging-drop of water frequently send out a short promycelium upon which these bodies are borne the second or third day after germination.

It has been observed that in old cultures on bean stems, especially in those that have been repeatedly transferred, the acervuli become less prominent, in fact scarcely make their appearance at all; but an abundant stroma is developed. This peculiarity corresponds apparently to the habit of the fungus on its natural host, for in the older pustules, in which the ends of the basidia have grown out in long, dark colored filaments, the

production of conidia seems to have ceased, and the ends of the hyphæ terminate in the enlarged bodies.

The Glœosporium found on the quince produces also a dark brown depressed spot which increases by well-marked concentric rings. The tissue remains quite firm, becoming more or less hardened, and frequently cracks. In the growth characters of the colonies, and in the habit on bean stems, the resemblance to the species found on the apple is so close as to leave no doubt that the two fruits are infested by the same species; the slightly different effect produced on the host being doubtless accounted for by the firmer tissue of the quince. Professor Halsted[5] further confirmed the identity by inoculating the quince with "virus" obtained from the apple. The writer has also successfully transferred the Glœosporium from the quince to the apple. However, since these forms easily adapt themselves to artificial cultures and are in a measure saprophytic, too much importance should not be attached to the results of laboratory inoculations, where the conditions are more or less artificial.

No indication of a yeast form has been found in connection with the development of the species.

GLŒOSPORIUM PHOMOIDES Sacc. (*figs. 5–7, 39–41*); on tomato (*Lycopersicum esculentum*).

An anthracnose causing a ripe rot of the tomato is manifested at first by a small circular depressed area. Older spots show a lighter central portion surrounded by a dark marginal band 2–3^{cm} in diameter. Upon the central portion, the dark-colored fruiting pustules first appear, producing irregular fissures in the epidermis, which often turns a bright yellow on the margins. From the pustules the conidia ooze out in light pink masses. With age the diseased portions become quite black.

The spore measurements vary considerably from those given in Saccardo (**3**: 618), some of them measuring 18.5 × 5–6 μ. In shape they may be oblong, elliptical, fusoid or reniform, and sometimes curved.

[5] N. J. Ag. Exp. Rept. 316–317.

The acervuli in section bear little resemblance to those of the ripe rot of apple. From a well developed cup-shaped stroma, lying some distance beneath the epidermis, the short continuous basidia arise. They do not project beyond the host, but the conidia are delimited beneath the epidermis. Although the acervuli may be closely adjacent, they seldom become confluent, and the structural characters maintain a greater uniformity than is seen in *G. fructigenum*.

In dilution cultures with meat- or potato-agar, however, the two species resemble each other in the early appearance of the colony. The conidia of *G. phomoides* germinate readily, frequently becoming once septate. The colonies show the dense, elongated, Y-shaped, or stellate center; the marginal growth does not present the regular, more or less parallel arrangement of hyphæ seen in *G. fructigenum*, although this character depends somewhat on external conditions. With age, however, the roseate tinge of the colony is less marked. The mycelium is nearly or quite white until a stroma begins to develop. This usually makes its first appearance in a circle about midway between the center and the margin, when the colony is from six to nine days old. This extends gradually both toward the center and the margin of the entire colony, frequently becoming in time a dark reddish-brown. In parallel cultures of the two species this difference is more marked in potato- than in meat-agar. In meat-agar the mycelium approaches the buff-pink tinge seen in *G. fructigenum*, but here also a stroma is conspicuously developed. So uniform is this feature that it seems a valuable specific character. On bean stems the mycelium is a grayish-white at first, rather long and spreading; an abundant stroma is developed subsequently, which discolors the stems with thin, spreading, elliptical patches; upon these the dark fruiting pustules are situated. While the appearance on the stems is suggestive of the Gloeosporium of the apple and quince, in parallel observations of the two, the Gloeosporium of the tomato was distinguished by the darker fruiting pustules, and the duller tint of the conidium mass. At different times, however, and under

slightly varying conditions of the infusion of bean stems, these characters were found to vary and were not regarded as of so much importance as the characters developed in Petri dishes. Notwithstanding the fact that this fungus has been found to grow on the apple and quince in laboratory inoculations, the characters manifested in artificial cultures are sufficiently distinct, so that it seems to merit a distinct specific name.

Another disease appearing on maturing tomatoes causes the fruit to crack. These fissures are filled with an abundant white mycelial growth. The conidia are elliptical, oval, or fusoid, and resemble those of *G. phomoides*. On making a dilution culture it was found that the conidia were borne in chains, and proved to be the *Oidium lactis*.

GLŒOSPORIUM VENETUM Speg. (*figs. 8, 42–46*); on *Rubus* sp.

The raspberry is a most generous host for the anthracnoses, and the different genera and species parasitic upon it have formed an interesting group for study.

The most destructive of these, *G. venetum* Speg., has already received considerable attention from economic mycologists, and a brief description of the external characters of this species will suffice. The disease is said to attack all parts of the plant, even the fruit, although so far as the observations of the writer extend, it has been confined to the stems and petioles of both feral and cultivated plants.

It appears first in small purple spots, the oldest ones being found near the base of the plant. As the spots increase in size they become grayish-white at the center, where the tissue of the host frequently becomes ruptured. Encircling the spot may usually be seen an elevated purple border. The disease seldom permeates deeply into the tissue of the plant, but is located chiefly in the cambium layer, where the cells become shrunken and brown.

The conidia form amber colored masses on these spots, and upon examination may be distinguished easily from the other species on the raspberry by their small size. They are oblong-

elliptical, measuring 5–7 × 2.5–3μ. The short basidia, which soon become erumpent, spread over the spot and are not confined to a definite pustule.

The fungus does not adapt itself readily to artificial culture, and considerable difficulty was experienced before obtaining a pure culture. The conidia are not easily distinguished from isolated yeast cells, and a fungus forming light colored masses on the anthracnosed spots, and producing conidia closely resembling the conidia of *G. venetum*, proved to be a yeast form.

The conidia germinate readily in water or agar, but after the germ tube has attained a length of three or four times the length of the conidium, further development is very slow. In agar, numerous short branches are sent out from the primary germ tubes, which become closely septate; the cells, including the conidium, become somewhat swollen, so that the conidium itself can be distinguished with difficulty from the cells of the mycelium. Separation is more or less difficult, since growth in acidified agar is even less favorable than in a neutral medium, and bacterial and other foreign growth is liable to contaminate the cultures before the colonies can be seen in order to be separated.

Many unsuccessful attempts were made to obtain a pure culture of the anthracnose of the raspberry.

As late as November 29 fresh conidia were again obtained. With some of these a culture was made in a hanging-drop of water; dilution cultures were also made in acidified and neutral agar. On the following day the cultures were examined and many conidia were found to be sending out slender germ tubes by which, in the crowded condition in the hanging-drop, the conidia were frequently fused; the tubes attaining three or four times the length of the conidium. Four days after sowing, the germ tubes in the Petri dish cultures had attained a length of 24–60μ. They were divided into cells but slightly longer than broad, which were swollen so that the mycelium presented a moniliform appearance. On December 2 transfers of blocks of agar containing germinating conidia were made to tubes of bean stems. The growth at first seemed very unpromising. Small

tufts of white mycelium appeared on some of the stems. By December 22 the growth had spread so as to form colonies about 2–3^{mm} in diameter. Very little mycelium could be seen, but one pink mass of conidia was borne on the upper portion of one of the stems. On examination the mass was found to be composed of closely packed basidia, bearing at the end elliptical or oval conidia 6–7μ in length, although occasionally one was found measuring 12 or 14μ. These were sometimes united by short germ tubes. Dilution cultures were made in potato-agar from this colony. Growth took place very slowly; some of the conidia gave rise to two or three germ tubes, these branched frequently and became closely septate. The resulting colonies did not advance beyond a diameter of 3–4^{mm}. At first they presented a stellate, or snowflake appearance, but later became quite dense and compact, with a close even marginal growth. The mycelium assumed a deep red color, darker at the center and shaded to a light pink toward the margin, and presented a glazed, shining appearance. The production of conidia was not observed. Subsequent transfers to tube cultures on bean stems, as well as on sterilized raspberry stems, resulted in a very slight mycelial growth in scattered tufts. Some of these tufts floated freely on the surface of the infusion, in small stellate colonies, and often became attached to the sides of the tubes. In connection with the mycelial growth were small, pink, elevated masses.

So peculiar was the growth and unlike that of any other species of anthracnose studied, that in order to satisfy myself that the growth was that of the anthracnose, fresh material was again obtained the following July. The growth in agar and on bean stems manifested the same peculiarities as before, but upon closer examination of the newly formed patches on the stems the conidia were found. These quickly fall away and form the small colonies which were before mentioned floating freely on the infusion. The colonies in agar did not attain a diameter of more than 3–4^{mm} when six or nine days old. They presented the same dark red or copper colored center with a compact

chocolate colored or dull pink margin. Upon teasing out the colonies and examining them under the microscope, the conidia were found in all stages of germination. Some of them presented a dumb-bell appearance, while in others the germ tube about equaled the conidium in diameter, so that it could scarcely be distinguished from the vegetating mycelium. This crowded growth, and the rapid germination of the conidia in the colony, probably accounts for the small size attained by the colonies and their dense, hard, interwoven character.

On sectioning portions of the bean stems upon which the fungus was growing, within the tufts of mycelium were found perithecia-like bodies with delicate walls of closely interwoven mycelium. These were quite small, measuring from 60 to 70μ in diameter, ovate or pyriform. The peripheral cells were light brown, the interior was filled with light colored cells rich in protoplasm. While this condition suggests an ascigerous stage in connection with the fungus, it has not yet matured.

On the hyphæ surrounding these bodies were developed buds or gemmae; these were smaller than those found in other species but were of the same general shape, and of a dark brown color.

Synonymy.—*Glœosporium venetum* Speg. is commonly regarded as a synonym of *G. necator* E. & E., the original distinction being that the former one affected the leaves while the latter was confined to the stems. This distinction is now seldom regarded, the description of the two as found in a natural state agreeing so closely that there is little doubt as to their identity. Not having obtained cultures from the fungus on the leaves, the writer is unable to discuss their growth characters in nutrient media.

Glœosporium naviculisporum, n. sp. (*figs. 11, 58–61*).

While attempting to obtain a culture of *G. venetum*, a species of Glœosporium was found on twigs obtained from Mr. Pearson, of Vineland, N. J. This proved to be quite a different species, although the conidia were obtained from canes quite badly affected with the characteristic spots caused by *G. venetum*.

The conidia of this new species are larger than those of *G. venetum*, measuring 12–15 × 4–6μ, in shape fusoid or navicular and sometimes curved.

Unlike *G. venetum* the fungus is a rapid grower, the colonies attaining, under favorable conditions, a diameter of 1^{mm} in three or four days. The colonies have a uniform growth of pure white, erect mycelium, resembling at first those of *G. fructigenum*. It is separated from this species, as well as from *G. phomoides*, by the navicular character of the conidia and by later growth characters. In addition to the characteristic development of mycelium, there are developed abundant bright pink acervuli, formed in concentric rings. It is also distinguished in its development on bean stems by the entire absence of stroma; this character was noted throughout many generations of cultures. The abundant mycelial growth noted in the agar-agar cultures was not so marked on bean stems, but large pink acervuli are freely developed and the conidia frequently sink to the bottom of the tube, where they form a thick, pink sediment.

The colored, club-shaped bodies have been noted in hanging-drop water cultures. Growth on bean stems was at first less vigorous than on sterilized raspberry stems, but in laboratory culture it gradually adapted itself to the former. Inoculations were made on cuttings of raspberry stems transplanted in the greenhouse from the garden, in order to ascertain whether the fungus would adapt itself to growth on living stems. Eighteen days after the inoculations were made the fungus reappeared on the stems, the withered petioles, and along the veins of the leaves. As it has since been found on stems obtained from the university gardens in connection with *G. venetum*, it would be unsafe to say that the appearance was due to the inoculation, since the mycelium might have been lurking in the tissue before the transplantings were made, although the canes were in an apparently healthy condition.

The fungus seems to be a different species from those that have been described, and presents also growth characters distinct from the species studied in artificial cultures derived from

different hosts. Unlike *G. venetum* the acervuli are not confined to spots on the host, but spread indefinitely over the stem or leaves. From the form of the conidia I propose the name *Glœosporium naviculisporum*, with the following diagnosis:

Acervuli erumpent-superficial, 60–240μ in diameter, not confined to definite areas on the host. Basidia elevated, hyaline, 30–35μ in length. Conidia fusoid-elliptical, straight or slightly curved; ends acute, hyaline, continuous, measuring 12–15$\times$6μ; oozing out in deep pink masses on stems and leaves of Rubus.

HAINESIA RUBI (West) Sacc.[6] (*figs. 10, 51, 52*); on *Rubus*.

Another fungus of the raspberry is described by Saccardo under the name *Hainesia rubi* (West) Sacc. (Syll. **3**:699). This species has been collected in various localities about Cornell University. It is found abundantly on the leaves of Rubus, and is associated with *Cæoma nitens* (æcidial stage of *Puccinia Peckiana*), although this fungus does not seem essential to its existence, since it will grow on artificial media in pure culture. The acervuli are subcuticular, soon subsuperficial, on both upper and lower sides of the leaf. At maturity the conidia ooze out in pale pink heaps.

In section the pustule has much the same appearance as that of *G. naviculisporum*, but the conidia have not the pronounced navicular form found in that species. The colonies have a growth strikingly similar however to that species. There is the same abundant growth of white mycelium which gives the colonies a uniform undifferentiated appearance. The species is fur-

[6] The species which Miss Stoneman has studied here is identical with that described by Ellis and Everhart as *Glœosporium rubi* (Jour. Mycol. **4**:52. 1888) associated with *Cæoma nitens* on Rubus from Mississippi. There has been no opportunity to compare this material with the European specimens, but since their habitat is identical (association with Uredineæ on Rubus), the difference in measurement of the spores, which is not very great, would not seem a sufficient ground for the separation of the species, if they are generically the same. The genus Hainesia has forked and branched basidia. This character is certainly not common in the American specimens which I have examined. While there is a strong probability that the American and European specimens are the same species, it is not possible at present to speak with certainty.—G. F. A.

ther distinguished from *G. naviculisporum* by the development of a stroma in old cultures on sterilized bean stems.

Glœosporium cactorum, n. sp. (*fig. 14*); on *Cactus* sp.

There is a member of the genus Glœosporium which infests the cactus in greenhouse cultivation. The acervuli are erumpent-superficial, pale pink, becoming dark colored, situated on dark brown, decayed spots. On the margin of the spots the acervuli become confluent, often forming a close ring surrounding the less gregarious acervuli of the central portion. The conidia are elliptical, with rounded ends, and measure 12–17 × 4–6μ.

The conidia germinate readily in nutrient agar, and growth takes place rapidly. The colony has a white, snowflake appearance, belonging to a group showing a loose, open growth at the center, with the slender radiating strands of mycelium growing from the central point. The growth of the mycelium above the surface of the agar gives the colony a downy or flocculent appearance. The marginal mycelium presents a less regular growth than is seen in the open centered colony of *Colletotrichum glœosporoides*, and the open center is usually less distinct. By comparing the colonies with those of *G. cingulatum* Atk. (see *fig. 26*) a close resemblance will be observed. The latter, however, differs in the looser, irregular marginal growth, as well as in morphological characters, which will be discussed more at length in connection with that species.

On bean stems a dense growth of white mycelium is produced, which shows later a slight development of stroma appearing along the edges of the stems. A well developed stroma is formed at the base of the acervulum. The conidia ooze out in light pink masses. Associated with the acervuli are compact stromata, forming dark spherical elevations on the stems. Their appearance suggests perithecia, but no indication of asci has been found in connection with the species. *Fig. 17* represents colonies of the same species collected from a different variety of cactus a year later.

GLŒOSPORIUM MUSARUM Cke. & Mass. (*fig. 11*), on banana (*Musa paradisiaca*).

The anthracnose of bananas is quite commonly found on ripe bunches of the fruit in warm weather. The fungus appears in roseate, innate, erumpent, gregarious acervuli on blackened spots of the fruit. These spots spread over the entire fruit, and the underlying tissue becomes disorganized. The conidia are elongate, ellipsoidal, rounded at each end, usually with a single vacuole, and measure 16–18×4 μ.[7]

The material from which the first cultures were made was obtained from Ellis & Everhart's N. A. F. no. 3178. Conidia from the material collected in July 1894 germinated readily when sown in November of the same year. Germination takes place in the ordinary manner, one or two germ tubes originating at or near the end of the conidium. The conidia remain single-celled upon germination. Growth is rapid and the first crop of conidia in potato-agar appears the second day after sowing. The colonies have at first a stellate appearance, which becomes more or less obscured with further growth. Hyphal growth is sparse at the center, and the mycelium radiates in more or less straight lines. The flocculent or feathery radiations extending from the center to the margin give the colony a characteristic appearance. It is at first grayish in color, and assumes a buff tinge when the acervuli appear, which are scattered irregularly over the surface. Very little mycelium is developed on bean stems, but a compact grayish mat spreads over the surface of the infusion. Over this mat, as well as on the bean stems, the acervuli are produced in great abundance. They are comparatively large and attended with the development of a stroma, which does not spread thickly over the stems as in *G. cactorum*, *fructigenum*, and *phomoides*. Its entire growth marks it as a species distinct from the others that have been studied. The fungus readily adapts itself to various nutrient media. Although growing upon soft tissue on its natural host it shows a vigorous growth

[7] The original description in Grevillea (**16**: 3), gives the spore measurements 12×4μ.

of mycelium and an abundance of acervuli when transferred to sterilized oak and grape stems. The development of the so-called secondary spores has not been observed in cultures of this species.

Glœosporium fœtidophilum, n. sp.[8] (*fig. 12*); on skunk cabbage (*Spathyema fœtida*).

The Glœosporium which was found to infest this host causes black depressed, elliptical spots on the spathes. In a microscopic section, the cell walls are found to be very much collapsed; with the exception of those cells just above the acervuli, which frequently retain their normal shape and color though elevated by the underlying mycelium, and causing pale elevated spots on the surrounding blackened portion. The acervuli remain covered for some time, and the customary basal stroma is lacking; the mycelium forms an irregular, loosely interwoven mass at the fruiting points, the conidia being borne some distance beneath the surface, frequently filling the large intercellular spaces. They are slender, elliptical, and slightly inequilateral, varying in size from $7–12–15 \times 2–3\mu$.

Conidia sown in a hanging-drop of water become closely granular or vacuolate, usually once septate and frequently swollen at the ends, previous to germination. They send out two or three germ tubes which produce conidia quite close to the mother conidium. In potato-agar the growth is much more vigorous, as many as five germ tubes having been observed to originate from a single conidium. These branch frequently in a monopodial fashion and the conidia are abjointed so abundantly as to give the colony a yeast-like appearance. The colony is characterized by the pronounced stellate radiations which remain quite distinct from each other in the earlier growth, but the outspreading mycelium becomes more or less intermingled, rendering the radiations less pronounced. About 2^{mm} from the center these radiations branch profusely, giving to the colony a more or less uniform margin. The colony which is at first quite white assumes with age a pale yellow tinge.

[8] Collected by Professor G. F. Atkinson, Ithaca Flats, April 10, 1896.

On bean stems there is scarcely any development of mycelium. The conidia do not remain collected in heaps, but spread over the stems or collect in a dense layer on the surface of the infusion. The cultures in the tubes are also characterized by the uniform yellow tinge. No stroma develops in the cultures, and the colored club-shaped bodies are not formed either in agar, in bean stems, or in a hanging-drop.

The characters are as follows: acervuli for a long time covered, finally erumpent, situated on black depressed spots. Basidia short; conidia sometimes borne on intercellular hyphæ, hyaline, elliptical, ends acute, 7–12–15×2–3μ. On spathes of *Spathyema fœtida*.

GLŒOSPORIUM NERVISEQUUM (Fckl.) Sacc. (*figs. 13, 53–61*); on oak (*Quercus*), sycamore (*Platanus*).

This species may be easily recognized on the host by the shrunken withered veins of the leaves bordered by arid brown patches. The fungus causes the leaves to curl and become much distorted in appearance. The conidia, which may be found from early in June until November, are distinguished from the usual type of Glœosporium by their ovate pyriform contour, some being so constricted at one end as to appear almost stipitate. Others are more regular in shape, ovate-oblong or oblong, measuring 10–12×4.5–5μ.

Owing to the slow growth after germination has taken place, considerable difficulty was experienced in obtaining a separation culture, as it was closely associated upon the leaves with cladosporium, a pycnidial form, and other rapidly growing fungi.

In several unsuccessful attempts to obtain a culture from affected oak leaves, a peculiarity in germination was observed; the germ tube, which had a bulbous swelling at the base, made a short curve near its origin, sometimes encircling the conidium in a close coil. After germination had been observed the pieces of agar containing the germinating conidia were transferred to infusions of oak leaves. No satisfactory growth, however,

resulted from these cultures, which were made early in October, and they were discarded. On October 28 a Glœosporium was found on the leaves of a sycamore on Ithaca Flats. The veins of the leaves had the withered appearance and were bordered by the irregular patches which characterized the disease on the oak. Upon the under side of the leaf brown acervuli were produced, on which an abundance of conidia were found. The acervuli were not confined so closely to the region bordering the veins as was the case on oak leaves, and the withered portions were more expanded, but the color of the pustules, and the spore measurements were the same, and the same peculiarity in germination was noted, the germ tube frequently coiling once and a half or twice around the conidium. The fungus was less contaminated on the sycamore, and the growth could be more satisfactorily observed. On the day following the sowing of the conidia many were found to be germinating, sending out one or two germ tubes. On the third day after germination from three to five tubes could be seen to issue from a conidium which had in some cases become once septate, and the cells were slightly swollen.

The colonies in nutrient agar produce a rather scant mycelial growth, the clusters of conidia forming grayish masses for the most part submerged in the agar, are borne quite uniformly over nearly the entire colony. The colony has a loose, feathery, almost uniform growth, there being no marked radiations or abundant central growth. In both meat- and potato-agar the growth is slow. On bean stems, also, there is a very slight, inconspicuous growth of mycelium, and the tube cultures are marked by the pale brown acervuli which are produced quite freely on the stems.

In the following June (1896), material was again studied from diseased oak leaves; the appearance on the leaf and in section, as well as the peculiarity of germination and the growth developments in Petri dishes and test tubes, are sufficient evidence that the same species of Glœosporium infests both sycamore and oak.

COLLETOTRICHUM GLŒOSPORIOIDES Penz. (*figs. 15, 84*); on orange (*Citrus aurantium* L).

This disease, which was found on an orange tree in the conservatories, is also said to infest plants in outdoor cultivation. It causes, at first, light green spots on the leaves, which become collapsed and brown. Upon them are situated the black fruiting pustules which occur on both the upper and under surfaces of the leaf. Some spots show the acervuli arranged in quite regular circles around the margin, surrounding more indefinitely located acervuli at the center. The acervuli increase rapidly when the leaves are placed in a moist chamber, and the conidia ooze out in bright pink masses. They are rather broadly oval, 12–16 × 5–6μ, with one or two large oil drops. In section the acervuli, from 120–270μ in diameter, are seen to be erumpent, superficial, possessing a well-developed basal stroma, which gives rise to short basidia. The setæ, when present, are marginal, flexuous, once or twice septate, attaining a length of 130μ.

On bean stems the fungus develops an abundant loose, white, flocculent mycelium. The conidia ooze out in large masses, of a deep pink or orange color; a blackened stroma is developed quite abundantly, and the growth resembled that of *G. fructigenum*, of which parallel cultures were studied. Subsequent cultures, however, developed quite different characters in the colony than those of that species. The compact center developed in *G. fructigenum* is not seen in *Col. glœosporioides*. From the small central point of the colony of the latter species the mycelium radiates in from two to five directions. The branching of the mycelium is more or less suppressed at the center until the mycelium attains a growth some distance from the center. It there branches abundantly, the branches spreading out in a fan-shaped growth. These marginal tufts for a time remain quite distinct, but in older colonies well supplied with nutriment they mingle more or less, forming a continuous circular margin. The clear spaces at the center usually remain. The fruiting clusters appear in a circle some distance from the center. More or less of a stroma is developed in connection with the acervuli, so that

they appear as black points in the white mycelium. At times there is a pink pigment developed, which gives color to the acervuli. In subsequent transfers to bean stems, in which the mycelium was less abundantly developed, the pustules showed a considerable formation of stroma, and setæ were distinctly seen, although their presence is quite variable.

COLLETOTRICHUM LAGENARIUM (Pass.). Sacc. and Roumg. (*figs. 17, 18, 62–69, 75–79*); on watermelon (*Citrullus vulgaris*).

In Farlow's host index this species is recorded for the following cucurbits; watermelon (*Citrullus vulgaris*), muskmelon (*Cucumis melo*), cucumber (*Cucumis sativus*), pumpkin (*Cucurbita pepo*), and squash (*Cucurbita* sp.).

Its presence is indicated by subcircular brown spots on the rind of the watermelon; on some spots the tissue at the margin may become black, or the order may be reversed and a dark center may be surrounded by a lighter brown portion. Dull roseate acervuli rupture the epidermis, and are arranged more or less concentrically. The presence of setæ is a variable character; in some pustules which were quite mature none could be detected even in carefully prepared microscopic sections. This has led to some confusion in the history of the fungus as to its generic position. The conidia are rather long, narrowly elliptical, 16–20 × 4–5μ, sometimes ovate-oblong or inequilateral.

A section through the pustule shows but a slight development of basal stroma; the basidia are rather long, immersed, but extending partially above the surface of the host.

The fungus does not adapt itself readily to artificial cultures, and several unsuccessful attempts were made before satisfactory results were obtained. Conidia sown in meat-agar were seen to germinate, but subsequent growth took place slowly, and the contents showed disintegration. The mycelium became coarsely granular, and the contents showed disintegration. More satisfactory results were obtained in potato-agar, but here, also, the growth, as well as on bean stems, made but little progress at

first. With successive generations, obtained by making transfers of cultures, the fungus became gradually adapted to artificial conditions, and vigorous growth was obtained in potato-agar.

A normal type of germination takes place; one or two germ tubes arise from near the ends of the conidium, making their first appearance within six or twelve hours after the sowing is made. Twenty-four hours after sowing the conidia have usually all germinated.

The contents of the conidium become coarsely granular, and a clear space at the point of origin of the germ tube is seen as its contents pass into the tubes. The mycelium becomes coarsely granular or vacuolate, and branches in an irregular monopodial fashion. As the colonies exhaust the nutrient medium large hyaline vesicles appear as offshoots of the mycelium, or short branches of the mycelium become very much enlarged at the tips. The colonies make their first macroscopic appearance as small, irregularly stellate bodies; as they become older, the mycelial growth is nearly uniform, radiating from a small, dense central point. The conidia are first formed most abundantly at the center of the colony, where a pink acervulus appears. When the colony attains the age of five or seven days, the acervuli are formed irregularly over the central portion of the colony, the marginal mycelium keeping some distance in advance of the fruiting portion. The setæ are produced quite abundantly on the acervuli; in fact, the characters of Colletotrichum are often more distinctly manifested in artificial cultures than in a natural state. At the center of the colony a compact, reddish-brown stroma is formed, which does not spread far over the colony; beyond this stroma the colony acquires uniformly a buff or salmon tint. Faint concentric markings are sometimes seen in the colony.

Transfers to bean stems give rise at the point of inoculation to a spreading, grayish mycelium which covers the stems and the infusion. About three days after sowing the pustules appear in circular, elevated masses of a dull pink hue. As the culture becomes older they become surrounded by a stroma which gives

them a blackened appearance at the margin, and long setæ project some distance above the mass of conidia; these are dark brown except at the base, which is nearly hyaline, and they are frequently once or twice septate. The stems become blackened with a coarse, dark stroma, of irregular, more or less swollen cells, often terminating in club-shaped bodies. The mycelium does not develop below the surface of the infusion, but forms a compact coating over the surface which becomes glazed and shining, and of an intensely dark, reddish-brown color, becoming almost black, retaining, however, a reddish, iridescent hue.

The Colletotrichum on cucumber agrees so closely in all the growth characters that parallel cultures of the two in agar or on bean stems cannot be distinguished from each other. The similarity of growth leaves no doubt as to the identity of the species found on the two hosts, although the illustration of the two in section, and the appearance which the fungus gives to the host, might lead one to suppose them distinct species.

COLLETOTRICHUM LINDEMUTHIANUM (Sacc. & Magn.) Scribner, 1887 (*figs. 19–20, 70–74*); on bean (*Phaseolus vulgaris*).

The history of the anthracnose of the bean has been an interesting one, and much discussion has arisen in regard to its position and nomenclature.

We have an account of its first observation by Lindemuth at Popplesdorf, 1875. It was described and named in his honor by Saccardo and Magnus in *Michelia* 1: 129, under the name *Gloeosporium lindemuthianum*. Owing to its economic importance it subsequently received considerable attention, and has been figured and described in various journals.

Professor Scribner (Rept. Veg. Path. 1887), records the presence of setæ in the acervuli, and suggests that the species be placed in the genus Colletotrichum. In the report of the United States Department of Agriculture, 1887, Mr. Galloway describes the fungus and mentions that the presence of setæ was constant, though very scarce in some cases, in all the material. He also

suggests that the species be transferred to the genus Colletotrichum or Vermicularia.

Under the title "Identity of anthracnose of the bean and watermelon,"[9] Dr. Halsted describes some interesting experiments in inoculation of anthracnoses. The anthracnose of the watermelon was easily transferred to the bean, and a third fruit, the citron, was made to receive the anthracnose of both bean and watermelon; and he therefore regards the anthracnose of bean and watermelon, as well as that of the cucumber and muskmelon, as identical. So different was the development of the watermelon anthracnose from that described by Professor Atkinson[10] for the anthracnose of the bean (*Colletotrichum lindemuthianum*), that the latter was compared in artificial cultures with *G. lagenarium*.

Some fusted beans of the Wardwell kidney wax variety were obtained and placed in a moist chamber to germinate. After the first pair of leaves had appeared on the stems of some of the seedlings, the anthracnose was manifested in the characteristic depressed patches. The center of the spots was of a light brown color, bordered by a reddish-brown margin. Scattered over the depressed portions were the small leather-colored pustules. The appearance on the host marked a difference in the species, the watermelon showing a more indefinitely spreading discolored portion of the host which is not depressed. The character of the pustules in section would give less evidence as to their identity; in fact, there is a similarity both in shape and position of the acervulus, as well as in the length of the basidia and character of the conidia.

Dilution cultures were made in acidified and unacidified agar. The former medium was unfavorable to growth, as none of the conidia germinated. Those in the neutral medium two days later showed signs of germination, while four days after sowing several were found in different stages of germination. The first evidence of activity was seen in the swollen condition of the

[9] N. J. Agr. Exp. Sta. Rep., pp. 347, 352. 1893.

[10] Bot. Gaz. **20**: 305–311. 1895.

conidium at either end, which gives it the appearance of being constricted at the center. This agreed with the peculiarity observed by Professor Atkinson, as did the further development of the colony and the appearance on bean stems.

In order to compare the development of the anthracnose of the watermelon and the bean, parallel dilution cultures were made of the two on March 15, in order that uniform conditions of growth might be obtained. The material from which the cultures were made was obtained from separation cultures of the two previously made on bean stems. On March 16 the conidia of *Col. lagenarium* had sent out germ tubes about ten times their length, while others were not so far advanced, being shorter than the conidium itself. Some of the conidia were provided with septa, one usually at the middle. A few of the conidia of *Col. lindemuthianum* showed short germ tubes, but many had only increased in size. Four days later the conidia, which had just begun to germinate, showed the characteristic dumb-bell swelling, and many of those which had germinated earlier were also seen to be considerably swollen, and many were once septate. From some of the conidia as many as four germ tubes had formed. A few which had produced germ tubes of considerable size showed no appreciable difference in size or shape; whether a change would come later could not be determined as they were obscured by the mycelial growth. While the spores of *Col. lagenarium* occasionally become distended, the pronounced dumb-bell appearance is not a feature of germination. The germination of *Col. lindemuthianum* resembles that frequently observed in spores of Marsonia, which are originally septate. As the colonies had exhausted the nutrient medium, the enlarged vesicles observed in the mycelium of *G. lagenarium* were seen in *G. lindemuthianum*. These were larger than those previously mentioned; they were frequently once septate, and sometimes sent out one or several short tubes.

Not only do these two species show distinct differences in early growth, but the mature colonies present a very different aspect. Instead of the salmon cast of the colony, it is at first

a pure white, with a later development of sepia colored stroma over the central portion, where the fruiting pustules are most abundantly developed. This portion of the colony is not confined to such a limited area as it is in colonies of *Col. lagenarium*; nor does the outer portion of the colony become tinged, but remains a distinct white.

On bean stems the stroma is also soon developed, causing a blackened appearance of the stems, upon which there is but slight mycelial development, but it forms a white mat over the surface, which for some time forms a marked contrast to the blackened stems. In cultures a month old this also develops a stroma.

Since making the original parallel cultures the two species have been subsequently studied in connection with others; and, from material collected at different times and localities, with uniform results. The colonies of the bean anthracnose leave the impression of a study in black and white, while that of the watermelon, one in pink or salmon and a dark reddish-brown. A comparison of the two is well shown in *figs. 17, 18, 19, 20.*

These various differences which are so marked, and which are quite constant under varying conditions of temperature, seem to show conclusively, notwithstanding previous results in inoculation, that the two are distinct species.

From experiments made by the writer, it would seem that very little dependence can be placed upon the results obtained from cross inoculations made in the laboratory. The host to be inoculated is placed in a moist chamber or under a bell jar, where the moisture of the fruit is conserved, and the conditions are then favorable for any fungus which is already lurking in the tissue to develop. On the other hand, it has been shown that the fungi of this group easily adapt themselves as saprophytes, and a watery fruit like the watermelon or citron, which has been separated from the plant, has lost to a degree the power of resistance, and becomes more or less of the nature of a culture medium.

Volutella citrulli, n. sp. (*figs. 24–25, 80–82*); an anthracnose of the citron.

From the Ithaca markets an anthracnosed citron was obtained. It was marked by light brown, subcircular, confluent patches thickly covered with black acervuli, from which the conidia oozed forth in light pink masses. In some of the sporodochia setæ were present, while in others they were wanting. The conidia are hyaline, single-celled, elliptical or clavate, sometimes slightly curved, $15–20 \times 3–4\mu$. From the general macroscopic characters, and the shape and size of the conidia, as well as from the nature of the host, the fungus was at first referred to *Colletotrichum lagenarium* (Pass.) E. & H. Further study, however, revealed quite a marked difference in the two species.

The pustule of the citron anthracnose has its inception in a dense stroma just beneath the epidermis, but it extends some distance above the surface of the host. In some cases the stroma extends up around the basidia, almost forming a covering as is found in the genus Vermicularia. Long basidia arise above the stroma; the elevated basidia and the marginal setæ, when setæ are present, would show a close relationship to the genus Volutella. The setæ are colored, two to three times septate, with a swollen base.

This species develops quite differently from that of the bean, or watermelon anthracnose in artificial cultures. In colonies the salmon colored pigment of *Col. lagenarium* is wanting, and the fruiting pustules are not so centrally located, but appear as light colored pustules more or less separated from each other and somewhat concentrically disposed. A stroma, instead of being centrally located as in the two previously under consideration, appears in clusters of peculiarly contorted sclerotoid bodies terminating in club-shaped cells. These masses are formed in concentric rings, intermingled with the fruiting portions. The mycelial growth radiates in quite straight rays from the center to the margin. The growth on bean stems also presents a different aspect from *Col. lagenarium*, just mentioned.

On the stems the mycelium is scarcely apparent, but with a hand lens it may be seen to form a very sparse growth of short threads spreading out on the inner surface of the tube. The stems bear blackened elevations which resemble perithecia in shape, but which have never been found to be associated with conidia. The conidia do not form large pustules on the stem, but can barely be distinguished as small light colored elevations. The surface of the infusion becomes coated with a light colored scanty growth of mycelium. Within this growth appear light colored elevations composed of aggregations of swollen cells which develop dark membranous enveloping walls, similar in appearance to the dark elevations on the stems.

While it is possible that the species *Colletotrichum lagenarium* infests the citron, the species in question is distinct from the one studied on the watermelon. There seems to be no species described in the genus Volutella which agrees with the one under discussion, and the name *Volutella citrulli* is proposed with the following description:

Acervuli elevated; basidia elongated, seated upon an abundant stroma rising above the tissue of the host. Conidia hyaline, single-celled, elliptical or clavate, sometimes slightly curved, 15–20×3–4μ. Setæ, when present, marginal, septate, with a swollen base. Forming light brown, subcircular, confluent patches on the rinds of citron (*Citrullus vulgaris*, var.).

COLLETOTRICHUM LYCOPERSICI Chester (*fig. 21*).

Another anthracnose of the tomato is described by Chester[11] as follows: "Spots depressed, circular, slightly discolored, center black, 5–10^{mm} in diameter, becoming confluent. Acervuli abundant, densely gregarious, rusty brown or black, applanate, 95–150μ in diameter. Setæ abundant, fuliginous, generally curved, rarely undulate or straight, gradually tapering, septate, 65–110μ, about 5μ at the base. Conidia oblong 16–22×4μ, averaging 18–20×4μ, hyaline, 2–3 guttulate. Basidia short, slender, 30–40μ, arising from a well developed basal stroma."

[11] Del. Agr. Exp. Sta. Rep. 4:60–62. 1891.

Material was obtained from tomatoes of the yellow variety growing in the Cornell University gardens, answering in general to Chester's description, with the exception that the setæ are sometimes absent, and the basidia are rather longer than the measurements given in the original description. The colonies are quite different from those of the Glœosporium on tomato, as well as from those of *Col. lagenarium*. There is a scant development of decumbent, spreading mycelium, with a strong tendency to concentric markings in the growth, where the mycelium is more erect and in tufts, surrounding black, spherical perithecia-like bodies which produce long setæ. These, so far as has yet been determined, are sterile. The conidia formed freely on the mycelium do not mass up in large heaps. Toward the margin clusters are formed of knotted and swollen mycelium bearing quantities of dark colored buds or gemmæ. These lie quite close together, but are more or less distinct. They resemble the colonies of the Volutella on citron in this respect. On bean stems very little mycelium is developed, but the stems are plentifully covered with black spherical or hemispherical pustules, which bear long setæ. In some of these bodies setæ are absent. These bodies seem to be sterile, like those described in the colonies on nutrient agar. On the surface of the infusion a light colored mycelium forms a thick compact mat which does not have a flocculent appearance. but which is rather smooth and shining, and shows white compact aggregations of threads which with age turn black as those on the stems.

Another Colletotrichum was found on muskmelon, which from the similarity in artificial growth developments was referred to this species.

Volutella violæ, n. sp. (*figs. 22–23, 85–89*); on violet (*Viola cucullata*).

The Volutella on the violet is manifested on the leaves of the host by pale brown patches surrounded by a dark brown margin. In the center of the spots the black pustules of the

fungus are formed, usually on the upper surface of the leaf, though they also occur on the lower side.

It is distinguished as a Volutella by the marginal setæ, and by the elevated character of the sporodochia, although in some cases the basidia are scarcely more elevated above the host than is found to be the case in some species of Colletotrichum. The conidia are continuous, hyaline, curved, acute at each end, measuring $15–21 \times 3–4\mu$.

Upon germination the conidium contents become coarsely granular, and a germ tube pushes out at or near the end on the concave side. Sometimes a second and a third germ tube succeeds the first. These soon become irregularly septate. With the growth of the fungus the mycelium becomes short celled and closely intermingled, forming at irregular intervals patches of stroma. The mycelium at these places, which is at first colorless, becomes irregularly swollen and colored; from the center of this mass the conidium bearing basidia are formed. Certain cells of the stroma give rise to the setæ, which are enlarged at the base, usually twice or three times septate. Large colored club-shaped bodies are formed at the ends of certain threads of the mycelium, which frequently form grotesque masses by elongation and budding.

The colony of the fungus is one of the most beautiful ones studied. Three or four days after germination the small colonies present a stellate appearance; this character is gradually effaced and the mycelium forms a uniform colony of compact radiating threads. The acervuli are confined to a central region in the colony, in irregular arrangement, where a pink pigment is developed. This gradually extends over the colony, changing to violet, and producing a beautifully iridescent play of colors.

In tube culture a sparse grayish mycelium spreads over the stems, and forms a compact shining mass over the surface of the infusion which displays the iridescence seen in the colonies. With age this coloring disappears in the tubes but is quite lasting in Petri dishes. This delicacy of coloring is less marked

in colonies produced from conidia, which have for some time become adapted to artificial culture.

On sterilized stems the fruiting stools are formed similar to those found on the leaves but of a more vigorous habit. The setæ attain a length of 320μ. From the acervuli the conidia exude in dull pink masses.

The early growth characters and the development of the pigment show a close relationship with that of the Volutella of carnations described by Professor Atkinson. The colonies, however, of the latter show in photograph more decidedly stellate characters in the mature colonies, while in the former the stroma and setæ are black, instead of hyaline as in that species.

VERMICULARIA CIRCINANS Berk. (*fig. 16*).

The anthracnose of onions, which occurs quite frequently on the white varieties, was first described by Mr. M. J. Berkeley.[12] An account was subsequently given of the same disease by Dr. Thaxter.[13] The disease first appears as a small black dot, usually on the outer scales, which becomes encircled by rings. These concentric markings are caused by the acervuli, which as the disease spreads are scattered with less regularity over the scale. The pustules are plentifully supplied with setæ, and the conidia ooze out in dull flesh colored masses. They are elliptical, slightly curved, or inequilateral, measuring 20–22 × 3μ.

A section reveals a remarkable development of a stroma extending down into the tissue to a distance of 250–300μ. This development extends above the tissue to some extent. There is not, however, a perithecium developed, and although the fungus has been placed among the Sphæropsideæ, the character of the pustule shows a close resemblance to those species of Colletotrichum in which an abundant basal stroma is developed, while the marginal setæ and the elevated basidia, as well as the characters in artificial cultures, intimately associate the fungus with the genus Volutella.

[12] Gardener's Chronicle **11**: 595. 1851.

[13] Conn. Agr. Exp. Sta. Rep. **13**: 163. 1889.

In germination the protoplasm pushes out through one or more germ tubes usually near the end of the spore, in the usual manner. The colony, as it first appears to the unaided eye, presents a somewhat stellate appearance, but later from the point of inoculation a nearly uniform appearance is presented over a larger part of the colony, with a delicately fringed margin of spreading mycelium. The mycelium which grows both above and below the surface of the agar is at first nearly colorless; with age it becomes a dark smoky color. The discoloration usually appearing some distance from the point of inoculation, extends outward in irregular radiations. The ends of the threads become enlarged, colored, and delimited by a septum. These enlargements are also intercalary and at times peculiarly lobed and branched. At the center of the colony are grouped the dark colored fruiting bodies. At these points a stroma is formed and from some cells of the stroma setæ are borne as in nature. On bean stems the fungus produces a grayish mycelium which spreads over the surface of the infusion, becoming in time of a dark smoky color. A thin stroma spreads over the stems, and acervuli are produced abundantly, and are at times confluent. The setæ, which are quite conspicuous, are borne usually on the margin, sometimes at the center of the pustule.

ASCIGEROUS FORMS.

The course of development of many of the Ascomycetes, especially the Pyrenomycetes, is pleomorphic, and various conidial forms have been definitely interpolated with ascigerous stages. The structure and habits of the species of Glœosporium and Colletotrichum suggest that they too are form genera, having biological relations with perfect forms, although little has been definitely proven in this group to establish the connection.

Since the mycelial growth takes place largely near the surface of the host, and the conidia, provided with delicate walls, require no resting period previous to germination, evidence is strong that in the course of their life history, or at least in some

stage of their phylogenetic development, this group has, or once had, a complemental perithecial or pycnidial stage.

In 1886 Von Tafel[14] carried on some investigations with *Glœosporium nervisequum* (Fckl.) Sacc., which he suspected from morphological evidence to possess an organic relationship with a pycnidial form, *Discula platani* (Pk.) Sacc. Owing to the fact that the pycnidial form was always associated with the Glœosporium form on the leaves, he was led to suppose that the mycelium passed through the petioles to the branches and there formed the pycnidia whose conidia developed in turn the Glœosporium. He was unable, however, to establish the connection by cultures, and the question still remained an open one. In continuing the investigations there was a suggested connection of the Discula with an ascigerous form of the genus Fenestella. The apparent connection of this form with a second pycnidial form as well as with a form resembling Acrostalegma, tended to disprove rather than to establish the connection with the Glœosporium.

In connection with the study of *Glœosporium fructigenum* Berk., Miss Southworth[15] notes the finding of a perithecium containing two asci on the apple from which the Glœosporium was obtained, but the material, owing to contamination, could not be further examined. While the association of the two forms on the same host is interesting, very little value can be given to the incident in establishing a connection between them, for, as she says, the apple became contaminated and it is quite possible to account for the presence of the ascigerous form in that way.

Suggested connections are found in Saccardo's *Sylloge* of species of Glœosporium with ascigerous stages. *Gnomoniella? circinata*[16] on the leaves of Ribes is noted in connection with *Glœosporium ribis* and *Gnomoniella fimbriata* has been found associated with *Glœosporium carpini* on the leaves of Hedera.

In a large number of artificial cultures of *Glœosporium fructi-*

[14] Bot. Zeit. **44**: 284. 1886.

[15] Dept. Ag. Rept. Washington 348. 1887.

[16] Sacc. Syll. Fung. **1**: 416–419.

genum no perithecial form was found in connection with it by the writer. In the study of *G. nervisequum* (Fckl.) Sacc., both pycnidial and perithecial forms were found associated with it in the first dilution cultures, but when pure cultures were obtained by subsequent dilutions only the conidial form was found in the cultures.

It is an interesting and significant fact that two species of Glœosporium should be found associated with the same asciger-ous genus Gnomoniella. The writer made several attempts to obtain a culture of *G. ribis*, all of which failed and its culture was abandoned.

Gnomoniopsis cingulata Stoneman (*figs. 27, 28, 90–97*): *Glœospo-rium cingulatum* Atk. on *Ligustrum vulgare*.

In 1892 Professor Atkinson[17] described a new species of anthracnose of the privet (*Ligustrum vulgare*). The growth characters of the fungus in artificial cultures suggested the prob-able cycle of development of this Glœosporium. On cultures of sterilized bean stems the threads were associated into strands of compact tufts, several layers deep. Within these wefts were numerous black rotund perithecia-like bodies, white within and filled with rich protoplasmic contents, presaging, as the author suggested, a probable ascigerous stage. Subsequent to the pub-lication of this study, mature perithecia were obtained in pure cultures of this Glœosporium, sections of which were mounted and preserved. The material studied was obtained from Penn Yan, N. Y. The discovery of the perfect stage in pure cultures rendered the investigations of Professor Atkinson of more value than any results which had been previously brought to bear on the subject.

In February 1895, material was received from Manhattan, Kansas, through Professor Hitchcock, of the State Agricultural College. The affected stems showed the elongated depressed areas of a light brown color corresponding to the affected twigs originally described. No spores could be obtained owing to the

[17] Cornell University Exp. Sta. Bull. 49: 310. 1892.

age of the fruiting pustules, but with a flamed scalpel, after cutting away the surface tissues, portions of the affected areas were removed and transferred to tubes of sterilized bean stems on February 18. A grayish mycelium soon began to spread over the stems, and black perithecia-like bodies made their appearance in connection with the acervuli producing the masses of conidia. On March 18 an examination of the cultures was made, and the black elevated wefts of mycelium were found to be perithecia containing mature asci, agreeing in every respect with those previously mounted by Professor Atkinson.

The perithecia were cespitose, seated upon a subiculum or stroma of loosely interwoven mycelium, dark brown, flask-shaped, membranaceous, measuring from 250–320μ in length and about 150μ in diameter, gradually constricted toward the apex into a short rostrum. The perithecia were more or less hairy with a conspicuous tuft of coarse brown mycelium about the ostiolum. The asci were aparaphysate, clavate, sessile, measuring about 64 × 14μ. Spores eight, hyaline, elliptical, slightly curved, subdistichous, 20–28 × 5–7μ, usually with a clear spot at the center.

As it was impossible to say from what growth this result was obtained, it now remained to establish definitely the connection of the ascigerous stage and the conidial form. A dilution culture was therefore made in nutrient agar, and spores were marked which by their size and shape could be distinctly recognized as ascospores. These spores germinated in the same manner as do the conidia, by sending out a germ tube usually near the end, a little in advance of one originating near the opposite end. *Fig. 97* shows germinating ascospores eight hours after sowing; twenty-four hours later under favorable conditions they may attain a length of 500 or 600μ, showing indefinite septation and irregular branching. The germination of some spores may be retarded and the germ tube delayed until the day following the sowing, although the spores do not become altered in size or shape. On the second day after germination as many as four or five germ tubes may be seen to proceed from a single

spore. These usually become branched quite near their origin, but the center of the colony remains open and the radiating mycelial strands remain distinct from each other for about 2^{mm} from the center. Beyond this the mycelium branches in a brush-like manner, mingling toward the margin in a loosely spreading uneven fringe. The colonies produced from the ascospore had the same characteristic snowflake appearance described by Professor Atkinson for the colonies resulting from the conidia. From the tips of the mycelium the elliptical or clavate conidia are delimited as early as the second day after germination; the time, however, varies, depending upon the separation of the colonies and the amount of nutriment. When the colonies are well separated and growing in an abundance of nutriment, the formation of conidia is delayed. In artificial cultures the acervuli are sometimes attended with setæ, although they are not sufficiently abundant to characterize the genus as a Colletotrichum, and none have thus far been found in sections of the acervuli made from the host plant. Very little pigment is developed in the agar in connection with the formation of conidia, but ten or fourteen days after sowing the colony begins to show a development of stromata in small circular masses scattered indefinitely over the colony, which become elevated above the agar and overspread it with a grayish mycelium. These are filled with coarse granular protoplasm, and represent the early stage of the perithecia; the agar, however, usually dries away before they become mature, although asci have occasionally been found in them. These are formed in connection with conidia, alike on the colonies developed from either ascospores or conidia. Portions of the mycelium produced from marked spores were removed to cultures of bean stems, the colonies being sufficiently separated so as to insure pure cultures. These separation cultures produced the grayish mycelium, bearing conidia abundantly, which collect in pink masses. The mycelium after about ten days becomes a dark brown; numerous dark buds or gemmae (?) are formed, and the association of the perithecia-producing stroma becomes manifest within a week or

ten days after inoculation. The perithecia become mature when the cultures have attained an age of three or four weeks.

Again in November 1895 both stems and leaves were received from Kansas affected with *G. cingulatum* Atk. On the leaves the fungus appears in light brown arid spots, oval or fusoid, bordering the midribs. Fruiting pustules are formed on both surfaces of the leaf, though more abundantly on the upper surface. From cultures obtained from these conidia, ascospores were again obtained. The two forms have been obtained repeatedly in subsequent transfers made to preserve the species in artificial cultures, and definite connection of the two stages cannot be doubted. While the pleomorphic course of development can readily be traced, it cannot be said that one stage is necessarily intercalated between successive crops of the other.

Gnomoniopsis piperata Stoneman (*figs. 98–104*); *Glœosporium piperatum* E. & E.; on pepper (*Capsicum annuum* L.).

In October 1896, peppers affected with *Glœosporium* were received from Professor S. M. Tracy of the Mississippi Agricultural Experiment Station. The affected areas appeared as circular or oval spots in which pale yellowish fruiting pustules had ruptured the epidermis in elongated, irregular fissures, which were closely associated so as to be confluent at the older affected portions; around the margin they were arranged concentrically The conidia were elliptical to oval, measuring $12–23 \times 5–6\mu$. A dilution culture of the conidia was made October 10. The conidia germinated in the ordinary manner within twelve hours; subsequent growth was slow and lest the colonies should become contaminated transfers were made to bean stems on October 23, although at this late date no conidia could be found in the cultures. The colonies showed few positive characters, the mycelium growing almost uniformly from a small light colored central point, with the exception of a less abundant growth surrounding the center about $4–5^{mm}$ in diameter. On bean stems the fungus developed quite an abundant grayish mycelium, standing out in a flocculent mass. On the surface of the infusion it is of a lighter color, and is usually more compact than on the stems, although this

condition varies in different cultures; in tubes containing richer nutrient material there is a more abundant and more compact development of mycelium. This difference is quite marked in parallel cultures on bean stems and young bean pods. In the latter case the mycelium is very abundantly developed, quite or nearly concealing the fruiting pustules. In tube cultures made on October 23 pink masses of conidia made their appearance five days later. In connection with the pink acervuli many perithecia-like bodies were observed. From this series of separation cultures a second dilution culture was made. The colonies again showed the nearly undifferentiated mycelial growth with the exception of a less abundant growth about the center. This portion, which is nearly free from mycelium at first, becomes overrun as the colony advances in growth, but the colony always remains more open at this portion. The production of conidia was not delayed so late in the second series of dilution cultures, and a few were formed eight days after sowing. Whether their earlier appearance was due to the condition of the nutrient agar, or to the fact that the fungus was becoming adapted to artificial growth conditions was not ascertained. The aggregated conidia form pale acervuli scattered quite thickly over the colony with the exception of the lighter portion near the center. In cultures ten or twelve days old the conidia become much longer than normal, and once or twice septate. From these cultures in which the colonies were so separated that pure separation cultures could be with certainty obtained, transfers were made on November 18 to an infusion of bean stems. On December 15 an examination of the tube revealed fully developed perithecia in connection with conidial clusters and the colored club-shaped bodies. The perithecia were so covered by the mycelium that their presence was not detected until a portion of the growth was removed with a needle and examined with the microscope. In order to check the experiment a second sowing was made of conidia which had undergone desiccation in the laboratory for five months. These germinated and conidia and perithecia were obtained as before.

The perithecial form closely resembles that of *G. cingulatum* Atk. On first examination it was thought that, though of the same genus, a specific distinction existed in the more slender perithecia of the former and the smaller spore measurements. These characters vary, however, in different cultures, and the larger measurements of the perithecial stage of *G. piperatum*. E. & E. are common to the smaller perithecia and spores of the privet anthracnose.

Ascospores sown in nutrient agar produced the conidia, and later on perithecia, which matured in thirteen days in the agar cultures, the colonies from ascospores having the same appearance as those from conidia. These colonies differ from those of *G. cingulatum* Atk. in the more uniform growth and the compact interweaving of mycelium at the outer portion of the colony. A description of the perithecial stage is as follows:

Perithecia cespitose, thinly membranaceous, dark brown, of a lighter color toward the ostiolum, at least in younger forms, pear-shaped, hairy, situated upon or partly immersed in a light-colored stroma of loosely interwoven threads. Asci aparaphysate, clavate, sessile; sporidia eight, hyaline, single-celled, slightly curved, elliptical, subdistichous, 12–18 × 4–6μ.

Gnomoniopsis cincta Stoneman (*figs. 31, 110–114*); *Colletotrichum cinctum* (Berk. & Curtiss); on orchid (*Maxillaria picta*, *Oncidium* sp.).

In connection with a study of the leaf spot of the conservatory orchid by Mr. Paddock, a student in the laboratory, one of the affected leaves, when placed in a moist chamber, developed an anthracnose. The anthracnose had apparently no connection with the so-called "leaf spot" of the orchid, which is probably of non-parasitic origin.[18] Later other anthracnosed orchids were found in cold house cultivation on species of the genera Maxillaria and Oncidium, having a similar appearance on the

[18] The disease has been found by Mr. Massee (*Annals of Bot.* 9: 421. 1895) to be due to sudden changes of temperature causing a precipitation of moisture on the leaves.

leaf and in the growth characters manifested in artificial cultures. The pustules are erumpent, appearing on either surface of the leaf, indefinitely located on large, withered areas, or arranged in waving concentric circles. Conidia 12–15 × 3–4μ, elliptical, 2-guttulate. Setæ rising above the pink masses of conidia characterize the genus as a Colletotrichum, which agrees in other characters with the species described by Berkeley and Curtiss as *Glœosporium cinctum*. The setæ frequently nearly obscured by the abundant masses of conidia are doubtless in some cases absent.

On sectioning portions of the leaf, the Colletotrichum was found associated with a pycnidial stage and also a minute pyrenomycetous form. The perithecia of the latter measured 48–75μ in diameter, were flask-shaped, borne singly or in clusters of two or three, on both upper and under side of the leaf. The bases of the perithecia were wholly or partly submerged, the partially emerging necks causing minute elevations in the tissue of the leaf. The spores were immature, and in sections the characters could not be well determined; they were small, elliptical, slightly inequilateral, hyaline, single-celled, and measured approximately 6–7 × 2–3μ.

Dilution cultures of the conidia were made February 16. On February 17 germ tubes arising from one or both ends of the conidium had attained a length of 15–50μ. Laboratory dried conidia which were sown later required a longer period for absorbing nutrient material before germinating. Many showed no sign of germinating twenty-four hours after sowing, except in the coarsely granular contents of the conidia. These later, however, germinated in the ordinary manner. The young colonies resulting from the conidia present a small, white center, from which proceed five or six slender radiating strands of mycelium which branch out about 2^{mm} from the central point in fan-like tufts, remaining quite distinct in some colonies, while in others they mingle more or less at the margin, if the growth is luxuriant. The mycelium does not have such a loose, undulating growth as that of *G. cingulatum* Atk., which it resembles in

the open portion surrounding the center, but the colonies resemble those of the orange anthracnose (*Col. glœosporoides*).

On bean stems the fungus develops a pure white mycelium which in rich nutrient media covers the substratum with a close, white felt. In some of the tubes black perithecia-like bodies made their appearance on the stems, while in others they were mingled with pink acervuli, and again the acervuli appeared almost exclusively. On bean stems, to which transfers were made February 17, perithecia containing asci were found on March 21. In cultures two months old many of the perithecia-like bodies retain their white protoplasmic contents, the cessation of further development probably being due to the exhaustion of the nutrient media. The perithecia measure from 180–280μ in diameter, are flask-shaped, membranaceous, and cespitose. Asci aparaphysate, clavate, sessile, truncate or obtuse when mature, measuring 65–70μ in length, eight-spored. Sporidia hyaline, single-celled, elliptical, curved, measuring 15–20 × 3μ. From the germinated ascospores the conidia were again obtained. The first results were verified by cultures made later from different material.

The ascigerous stage, as may be seen by comparing the description and illustrations, bears a close resemblance to the two previous forms. The characters of the colonies show a specific distinction, as well as the general appearance of the fungus on the leaf and the presence of setæ in the natural state.

It is possible that the perithecial stage obtained in artificial cultures is identical with that found in connection with the Glœosporium on the leaf. The difference in size and the presence of a stroma might be accounted for by the artificial conditions of growth.

Gnomoniopsis rubicola Stoneman (*figs. 29–30, 105–109*); *Colletotrichum rubicolum* E. & E.; on red raspberry (*Rubus strigosus*).

In December 1895 some anthracnoses were kindly forwarded me by Mr. J. B. Ellis, among them a new species, at the

time unpublished, on *Rubus strigosus*, accompanied by the following description: "Forming large, dark brown patches on the upper surface of the leaf; sori small, dark, suberumpent; conidia oblong, elliptical, 12.5 × 6μ. Col. W. Va., Oct. '95, F. W Nuttall."

Conidia sown in a dilution culture of potato-agar on January 30, four hours later had developed germ tubes usually from one end of the conidium, and slightly constricted at the base, proceeding in irregularly flexous manner, occasionally septate, with little or no branching for a distance of 100–150μ. On January 16 the growth could be seen in the agar with the unaided eye, the low temperature of the laboratory possibly accounting for the slow progress of the fungus. The mycelium showed a long, narrow, loosely branched growth, 3–4^{mm} in length. A colony from one of the conidia, which had been marked at the time of germination, was transferred to sterilized bean stems. Four days later the mycelium had formed a rather dense, closely adhering weft of grayish mycelium; black fruiting bodies appeared upon the stems, which were also overspread with a mycelial growth. Upon examining these on February 10, the perithecia were found to contain mature asci, the ascigerous stage agreeing generally in appearance with the two previous forms. There is lacking in this species the conspicuous tuft of mycelium at the apex of the perithecia, which are usually larger than those of the pepper anthracnose.

The ascospores germinated in potato-agar, as had the Colletotrichum conidia, by sending out obliquely from one end a germ tube; the tube again is slightly constricted at the base, and extends from 180–200μ in length before branching takes place. This growth produces a colony, which, like that from the Colletotrichum conidia, is at first narrow, elongate, and loosely spreading. About four days after germination, conidia are delimited from the mycelium in great abundance. Later, colored swollen buds are formed. The reproduction of conidia here took place much sooner than in the original cultures of the conidia; and, inasmuch as the temperature of the laboratory

was nearly uniform at the two different times, their earlier appearance may be accounted for by its gradual adaptation to the artificial environment. Certain cells in the mycelium become swollen, usually septate and dark colored, and, in many cases, the fusion, with a smaller, curved, mycelial branch suggests a process of fertilization, although no careful study of this point was undertaken. From the swollen cells numerous colored branches arise which twine about and conceal it. At these places in the mycelium perithecia are formed.

The appearance of the colonies is quite peculiar to the species. The mycelium radiates from a small central point, in a feathery manner, forming one or two fan-shaped expansions which sometimes remain quite distinct for some time, or when growth proceeds in several radiations they become more or less united, and growth is more or less uniform. The margin of the colony has an even fringe of straight, nearly parallel threads.

The colony, which is at first flesh-colored, assumes a faint greenish tinge, which becomes a dark olivaceous brown at the more central portions, while the marginal growth retains the buff or slightly salmon tinge. The darker central portion is surrounded by the black fruiting bodies which are tufted with a grayish mycelium. The peculiar development of pigment is quite unlike that found in the three preceding species, or in fact in any species yet studied.

In connection with the perithecia grown upon bean stems, large conidial cushions were formed, surrounded with dark spreading hyphæ arising from a stroma at the base of the cushion. The conidia in artificial cultures frequently become septate.

Gnomoniopsis? vanillæ Stoneman (*fig. 32*); *Colletotrichum* on Vanilla.

An anthracnose was obtained from a vanilla plant growing in the conservatory which belonged to the genus Colletotrichum. It appeared in small black erumpent pustules on both sides of

the withered leaves, on the stems, and on the aerial roots. The pustules measured 150–180μ in diameter; a section through the pustules shows a well developed basal stroma, bearing closely crowded septate basidia 30–45μ in length. The setæ are colored, three or four times septate near the base. In older pustules the stroma passes up around the basidia, forming a cylinder of a compact association of rather regular rectangular cells. The pustules are somewhat superficially situated, the basidia extending nearly their whole length above the epidermis of the host.

Closely associated with the Colletotrichum was found a pyrenomycetous form. The perithecia bore a close resemblance to those described by Massee[19] in connection with another conidial form belonging to this group, the genus Hainesia. They were flask-shaped, having a membranaceous wall several layers in thickness, borne singly or in clusters, but without a stroma. Asci clavate, sessile, 75–80×15–16μ, attenuate at base, paraphysate, 8-spored; paraphyses long, slender, filiform; sporidia elliptical, hyaline, or slightly fuliginous, curved 21–24×6–7μ. The form described by Massee belonged to the genus Calospora, and differed in the presence of a stroma and in the tri-septate sporidia. The perithecia found on the leaves were not valsoid as in Calospora, but when two or three were aggregated the necks diverged.

The close resemblance of the two forms and the association of a Colletotrichum suggested an interesting study, and a dilution culture was made of the conidia in meat-agar. The leaves, which were more or less decayed, were an easy prey to saprophytic fungi, so that the first dilution was liable to be contaminated. The conidia, however, were found in great abundance in plates one and two, and germination was observed. Owing to their crowded condition, however, and the liability to contamination, these plates were discarded. Plate three contained but one colony. It had attained in eight days a diameter of 2^{cm} and was nearly uniform in growth. As frequently happens with a

[19] Kew Bull. Misc. Information 139: 111–120. 1892.

good supply of nutriment, when a profuse vegetative growth takes place, the production of conidia is delayed. Transfers, however, were made to bean stems in order to determine its further growth characters, and to avoid the possibility of contamination from exposure to the air. As germination had not been observed it was impossible to say from what the colony had originated.

On bean stems there was developed a rather compact white mycelial growth, and black fruiting bodies made their appearance in connection with the Colletotrichum conidia. The former developed into perithecia containing paraphysate asci with single-celled, curved spores. These spores when sown produced conidia, but from the conidia the perfect stage has not yet been obtained. Further investigation will be necessary in connection with this species, and a further detailed description will be deferred to another paper.

The colonies from both ascospores and conidia, in their uniform growth, with the exception of a slightly open growth around the central point, resemble those described in connection with *Glœosporium piperatum*.

CONCLUSIONS.

I will sum up briefly some of the more important results obtained in connection with this study: The group of fungi under discussion, commonly known as anthracnoses, in many cases present, in artificial cultures, distinct characters of growth for distinct species, which may be made of value in distinguishing species whose similarity in morphological structure in connection with their host often renders their systematic position uncertain.

The artificial growth characters of a single species fluctuate within certain limits with varying conditions of temperature and nutrient media, and certain characters which are prominent may become obscured with age, so that to render the characters of taxonomic value uniform growth conditions are essential.

The formation of the so-called secondary spores or buds

which are common to Glœosporium, Colletotrichum, Volutella, and Vermicularia is not a constant character, but may be absent throughout the entire cycle of development of a species, or they may be forced in these same species by a lack of nourishment.

The presence of a perithecial stage has been proven in four different species, of which the host plants vary widely in habits and structure. One of these exists as a saprophyte in a natural state (the one in connection with the vanilla anthracnose is omitted), while the other three are saprophytes in artificial cultures; whether they occur in nature has not been determined. Two of the perithecial forms were connected with species of the genus Colletotrichum, and two with Glœosporium.[20]

The colonies produced in the species with which perfect forms have been connected agree in producing a loose open growth about the center, but all show specific differences in formation of stroma, pigment, or arrangement of fruiting sori.

While the conidial forms show greater variations in structure than do the perithecial stages of the different species, the growth characters of the colonies from ascospores resemble those of the conidial stage with which they are connected more closely than they resemble each other.

The perfect forms approach the genus Gnomoniella, agreeing in the submembranaceous, subglobose, subcutaneous-erumpent perithecia; in the cylindrical, clavate, 8-spored asci; and the continuous hyaline conidia. They differ in the curved conidia, which in Gnomoniella are typically ovate, oblong subfiliform and straight, although in species of Gnomoniella, *G. amœna* (Nees) Sacc. and *G. fasciculata* (Fckl.) Sacc. they are curved. The genus under consideration does not show the slender, somewhat elongated beaks found in Gnomoniella, which are surrounded at the base with a white, cleft collar formed of the ruptured epidermis of the host, and the necks are hairy, while in Gnomoniella they are smooth. In shape the perithecia resemble the genus Camptosphæria, but they differ from this

[20] The presence of setæ in the cultures has been so variable as to raise the question whether they form a well-founded basis for distinguishing these two genera.

genus in other characters more than they do from Gnomoniella. Excluded from these two genera its position would be in a genus between these two for which the writer proposes the name Gnomoniopsis with the following diagnosis:

GNOMONIOPSIS, n. gen.

Perithecia cespitose, membranaceous, dark brown, rostrate, of a lighter color at the apex in early stages, flask-shaped, hairy, situated upon or partly immersed in a stroma; asci sessile, aparaphysate?, clavate, sporidia eight, hyaline, oblong, single-celled, slightly curved, elliptical, subdistichous, including the following species: conidial form, certain species of Glœosporium:

G. cingulata (p. 101), *G. piperata* (p. 104), *G. rubicola* (p. 108), *G. cincta* (p. 106), *G. vanillæ*? (p. 110).

From the evidence of these perfect forms it is probable that the genera Glœosporium and Colletotrichum have developed from one common ancestral genus of the pyrenomycetous form described above. Since of about thirty species studied but five have developed the complemental ascigerous stage, it is suggested that they have, to a large extent, become divorced from a perfect stage, and have become so adapted to environment that they are able to maintain themselves from year to year without the intervention of this stage. Many of the anthracnoses are parasitic on garden and orchard fruits, and are thus preserved with their host during the winter. Under less favorable circumstances the conidia may tide the fungus over, since they will stand a certain amount of desiccation. The stroma and sclerotia may also assist in ther preservation.

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Zeitschrift für Pflanzenkrankheiten.

EXPLANATION OF PLATES VII–XVIII.

The first plate is from photographs of the Petri dish cultures, generally of pure cultures, the colonies being natural size. The pen drawings are made to two different scales, the sections of hosts and the perithecia being made all to one scale, while the conidia and details of germination are made to another scale.

PLATE VII.

FIG. 1. *Glœosporium fructigenum* Berk. from apple; culture 1, three days old.

FIG. 2. Same, four days old.

FIG. 3. Same, from quince; culture 1, three days old.

FIG. 4. Same; culture 3, six days old.

FIG. 5. *G. phomoides* Sacc. from tomato; culture 1, three days old.

FIG. 6. Same; culture 3, six days old.

FIG. 7. Same; an old colony, showing development of the stroma.

FIG. 8. *G. venetum* Speg.; culture 3, one week old.

FIG. 9. *G. naviculisporum* Stoneman; culture eight days old.

FIG. 10. Same, or *Hainesia rubi* (West.) Sacc.
G. venetum, *G. naviculisporum*, and *G. rubi* all from *Rubus* sp.

FIG. 11. *G. musarum* Cke. & Mass.

FIG. 12. *G. fœtidophilum* Stoneman; culture six days old.

FIG. 13. *G. nervisequum* (Fckl.) Sacc. from *Platanus*.

FIG. 14. *G. cactorum* Stoneman.

FIG. 15. *Colletotrichum glœosporioides* Penz.; culture three days old.

FIG. 16. *Vermicularia circinans* Berk.; colony showing beginning of stroma.

FIG. 17. *Colletotrichum lagenarium* (Pass.) Sacc. & Roumg. from watermelon; culture five days old.

FIG. 18. Same; culture from another series nine days old.

FIG. 19. *C. lindemuthianum* (Sacc. & Magn.) Scribner; culture four days old.

FIG. 20. Same; culture from another series nine days old, showing the pronounced stroma which is absent from the colonies of *C. lagenarium*.

FIG. 21. *C. lycopersici* Chester from tomato.

FIG. 22. *Volutella violæ* Stoneman, plate culture.

FIG. 23. Same; older culture.

FIGS. 24, 25. *V. citrulli* Stoneman from citron; the same plate at different ages.

FIG. 26. *Gnomoniopsis cingulata* Stoneman; colonies from conidia taken from the stem.

FIGS. 27, 28. Same; colonies grown from four ascospores; *fig. 28* shows early formation of the stroma which bears the perithecia.

FIG. 29. *G. rubicola* Stoneman.

FIG. 30. Same; culture five days old.

FIG. 31. *G. cincta* Stoneman.

FIG. 32. *G.* ? *vanillæ* Stoneman; from culture four days old.

PLATE VIII.

FIG. 33. *Glœosporium fructigenum* Berk.; conidia germinating three hours after sowing.

FIG. 34. Same; twenty-four hours after sowing.

FIG. 35. Same; conidia sown in water producing colored buds and anastomosing mycelium in three days.

FIG. 36; Same; old mycelium in plate culture.

FIGS. 37, 38. Same; sections of old acervuli bearing large colored bodies at tips of basidia.

FIG. 39. *G. phomoides* Sacc.; conidia.

FIG. 40. Same; conidia germinating after twenty-four hours in agar.

FIG. 41. Same; section of pustule on tomato.

PLATE IX.

FIG. 42. *G. venetum* Speg.; conidia germinating in hanging drop.

FIGS. 43–45. Same; conidia germinated in agar three days after sowing.

FIG. 46. Same; section of acervulus.

FIG. 47. *G. naviculisporum* Stoneman; section of acervulus on host (*Rubus occidentalis*).

FIG. 48. Same; conidia.

FIG. 49. Same; conidia in hanging drop; *a*, anastomosing conidia; *b*, short basidium bearing a "secondary spore."

FIG. 50. Same; conidia in agar twenty-four hours after sowing.

FIG. 51. *Hainesia rubi* (West) Sacc.; section.

FIG. 52. Same; conidia germinating.

PLATE X.

FIG. 53. *G. nervisequum* (Fckl.) Sacc.; section of leaf showing acervulus on *Quercus alba*.

FIGS. 54–56. Same; conidia and early stages of germination.

FIGS. 57, 58. Same on *Platanus*.

FIGS. 59, 60. Same; conidia showing early stages of germination in agar.

FIG. 61. Same; conidia in agar twenty-four hours after sowing.

PLATE XI.

FIG. 62. *Colletotrichum lagenarium* (Pass.) Sacc. & Roumg.; conidia.

FIG. 63. Same; conidia germinated after twenty-four hours.

FIG. 64. Same; conidium which has been in agar three days showing no swelling.

FIG. 65. Same; conidium and mycelium four days old.

FIGS. 66, 67. Same; mycelium in culture five days old.

FIGS. 68, 69. Same; section of pustule on host.

PLATE XII.

FIG. 70. *C. lindemuthianum* (Sacc. & Magn.) Scribner; conidia.

FIG. 71. Same; conidia in culture twenty-four hours old.

FIG. 72. Same; conidia, and mycelium in culture four days old.

FIGS. 73, 74. Same; section of pustule on pod of *Phaseolus vulgaris*.

PLATE XIII.

FIGS. 75, 76. *C. lagenarium* (Pass.) Sacc. & Roumg. on cucumber; section of pustule.

FIG. 77. Same; conidia anastomosing in hanging drop culture.

FIG. 78. Same; conidia in agar.

FIG. 79. Same; seta enlarged.

FIG. 80. *Volutella citrulli* Stoneman; section of citron rind showing character of pustule.

FIG. 81. Same; conidia in various stages of germination.

FIG. 82. Same; stroma formed in clusters in colonies.

PLATE XIV.

FIG. 83. *Glœosporium fructigenum* Berk.; section of pustule on fruit of quince.

FIG. 84. *Colletotrichum glwosporioides* Penz.; section of leaf of orange with pustule.

FIG. 85. *Volutella violæ* Stoneman; section of affected leaf.

FIG. 86. Same; conidia germinating.

FIGS. 87, 88. Same; stroma in agar.

FIG. 89. Same; seta enlarged.

PLATE XV.

FIG. 90. *Gnomoniopsis cingulata* Stoneman; section of leaf showing acervulus.

FIG. 91. Same; conidia germinating.

FIG. 92. Same; conidia produced in culture two days old.

FIG. 93. Same; ascospores germinating.

FIG. 94. Same; seta and conidia in old cultures from ascospores.

FIG. 95. Same; stroma produced in cultures.

FIG. 96. Same; perithecia grown on bean stems.

FIG. 97. Same; asci.

PLATE XVI.

FIG. 98. *G. piperata* Stoneman; section of fruit showing pustule.

FIG. 99. Same; perithecia from bean stem culture.

FIG. 100. Same; asci.

FIG. 101. Same; ascospores before and after germination.

FIG. 102. Same; conidia.

FIG. 103. Same; beginning of stroma.

FIG. 104. Same; conidia from ascospores in agar.

PLATE XVII.

FIG. 105. *G. rubicola* Stoneman; ascospores.

FIG. 106. Same; ascospores germinating in agar.

FIG. 107. Same; ascus enlarged.

FIG. 108. Same; beginning of formation of stroma in which the perithecia are developed.

FIG. 109. Same; section of perithecia grown on bean stems.

PLATE XVIII.

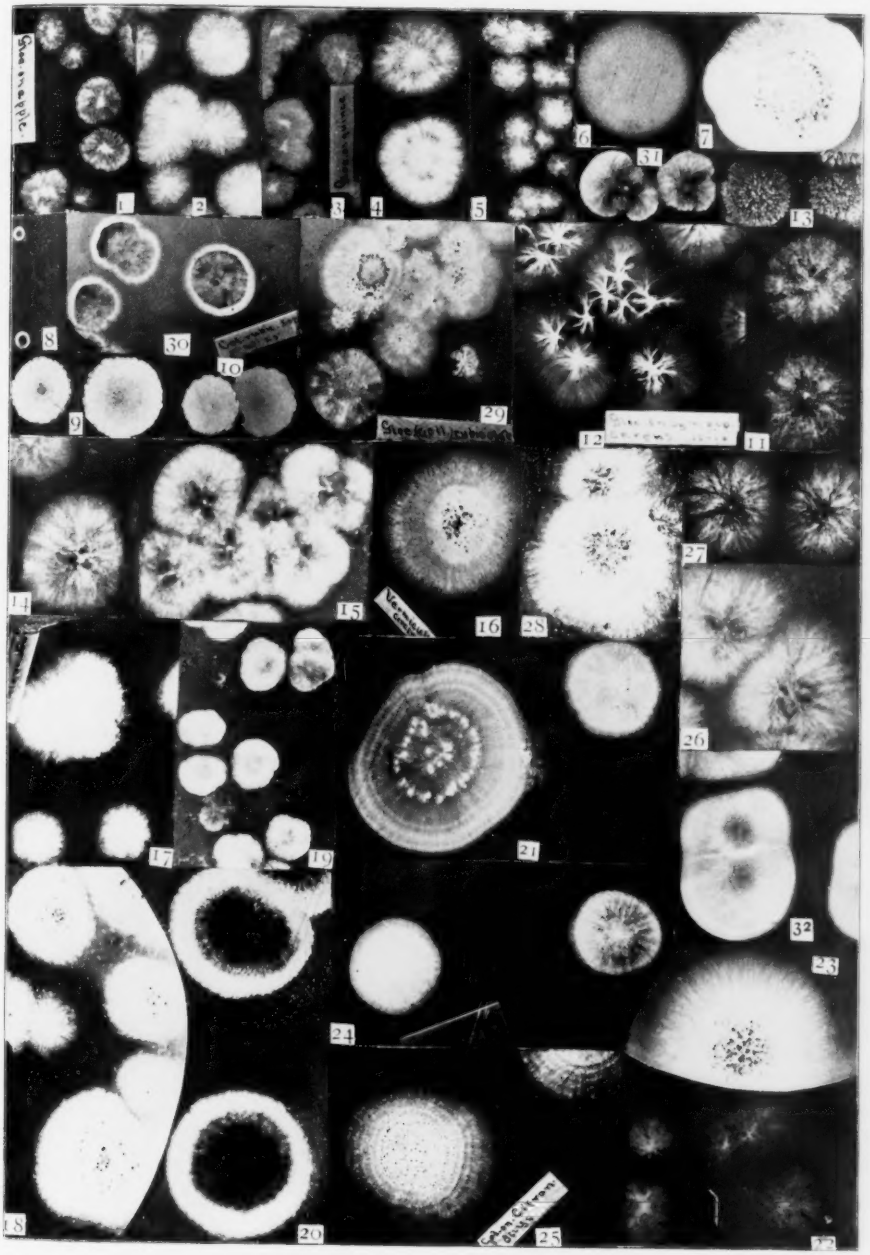
FIG. 110. *G. cincta* Stoneman; section of acervulus on leaf.

FIG. 111. Same; conidia germinating.

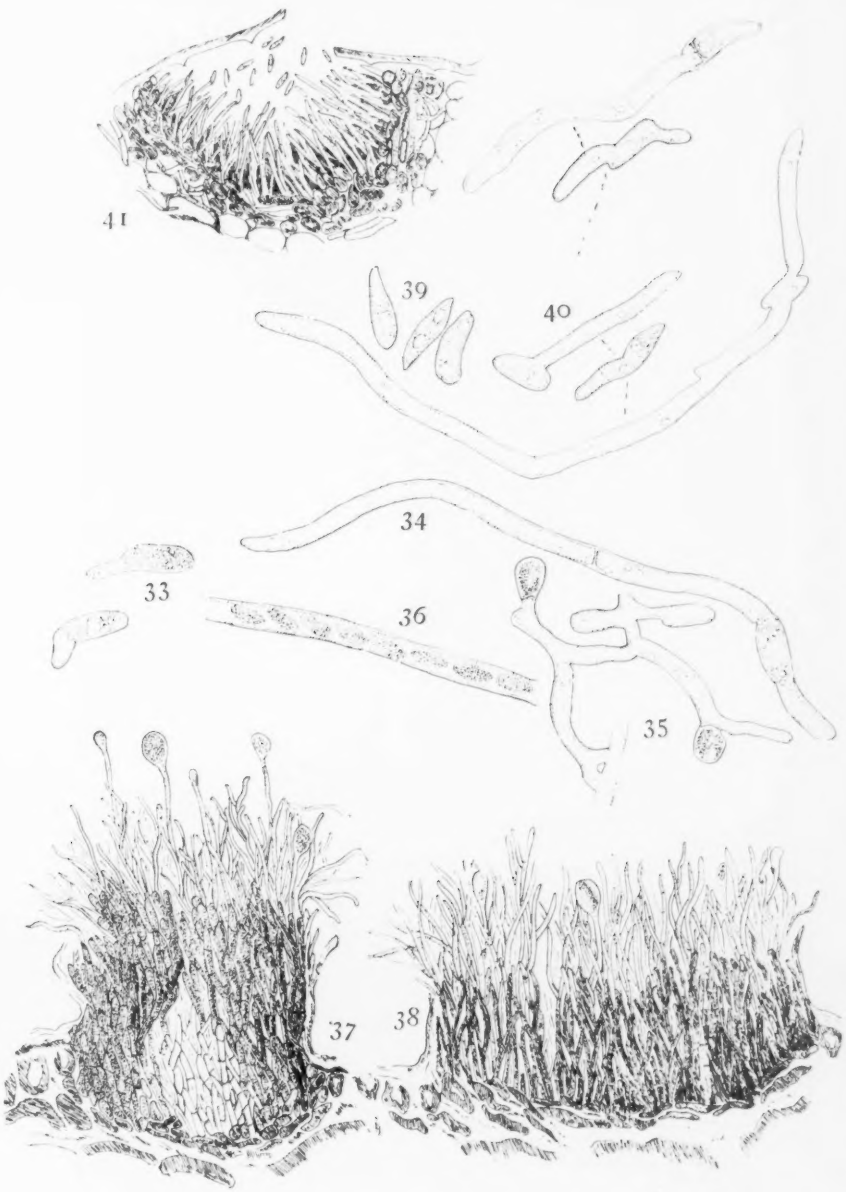
FIG. 112. Same; perithecia found on leaf of orchid in conservatory.

FIG. 113. Same; perithecia grown on sterilized bean stems.

FIG. 114. Same; immature ascus, and mature one with ascospores.



STONEMAN on ANTHRACNOSES



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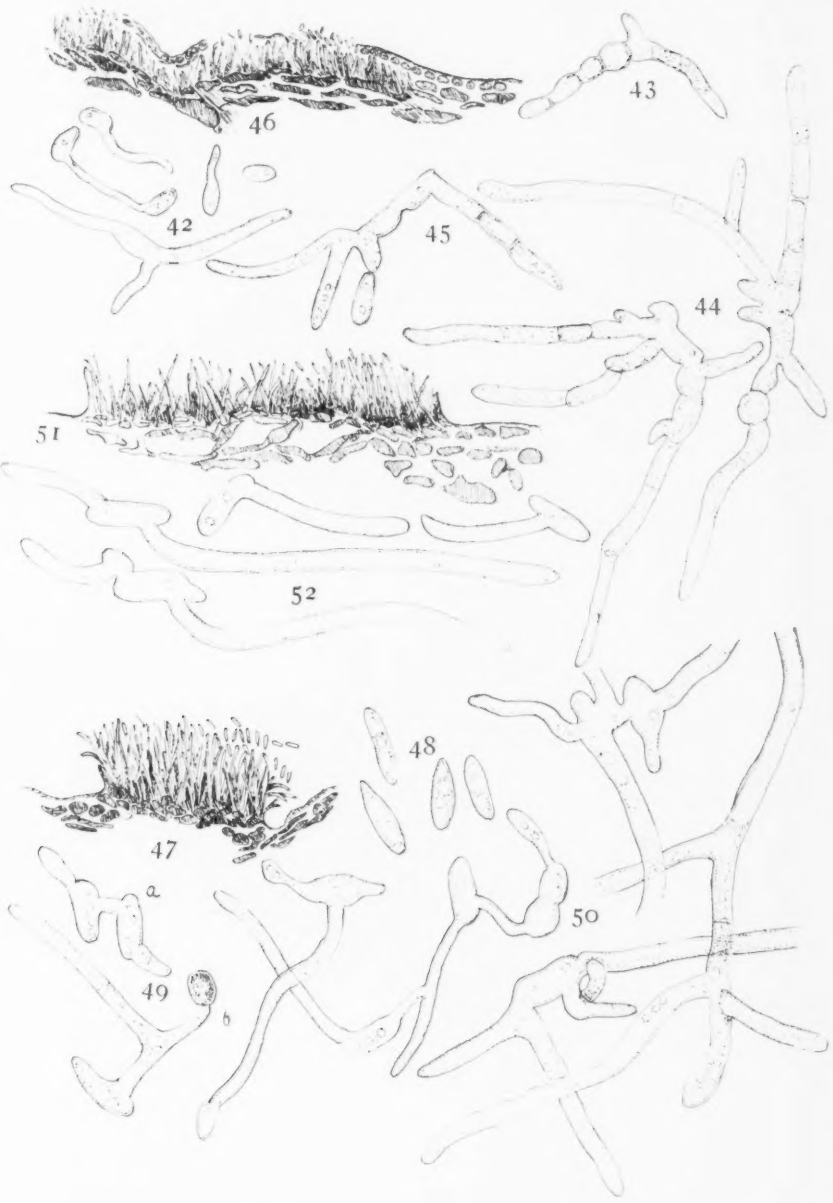

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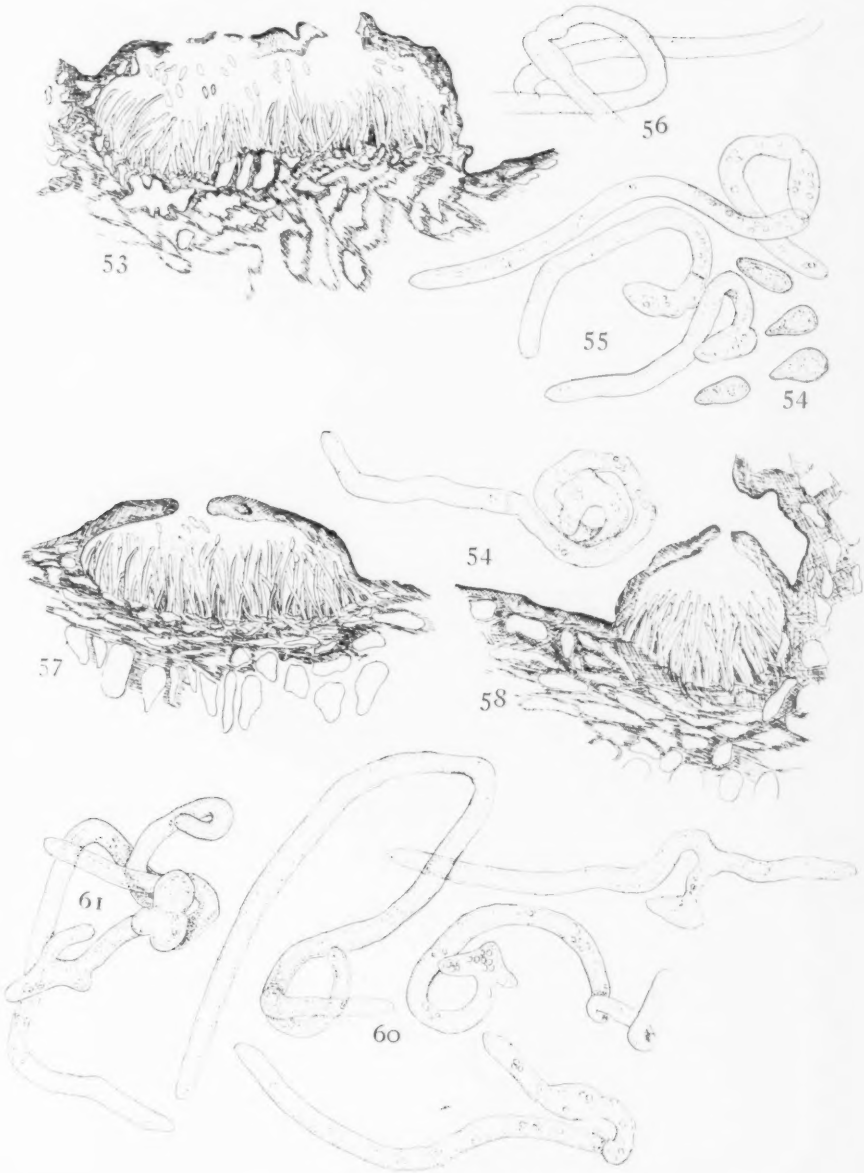

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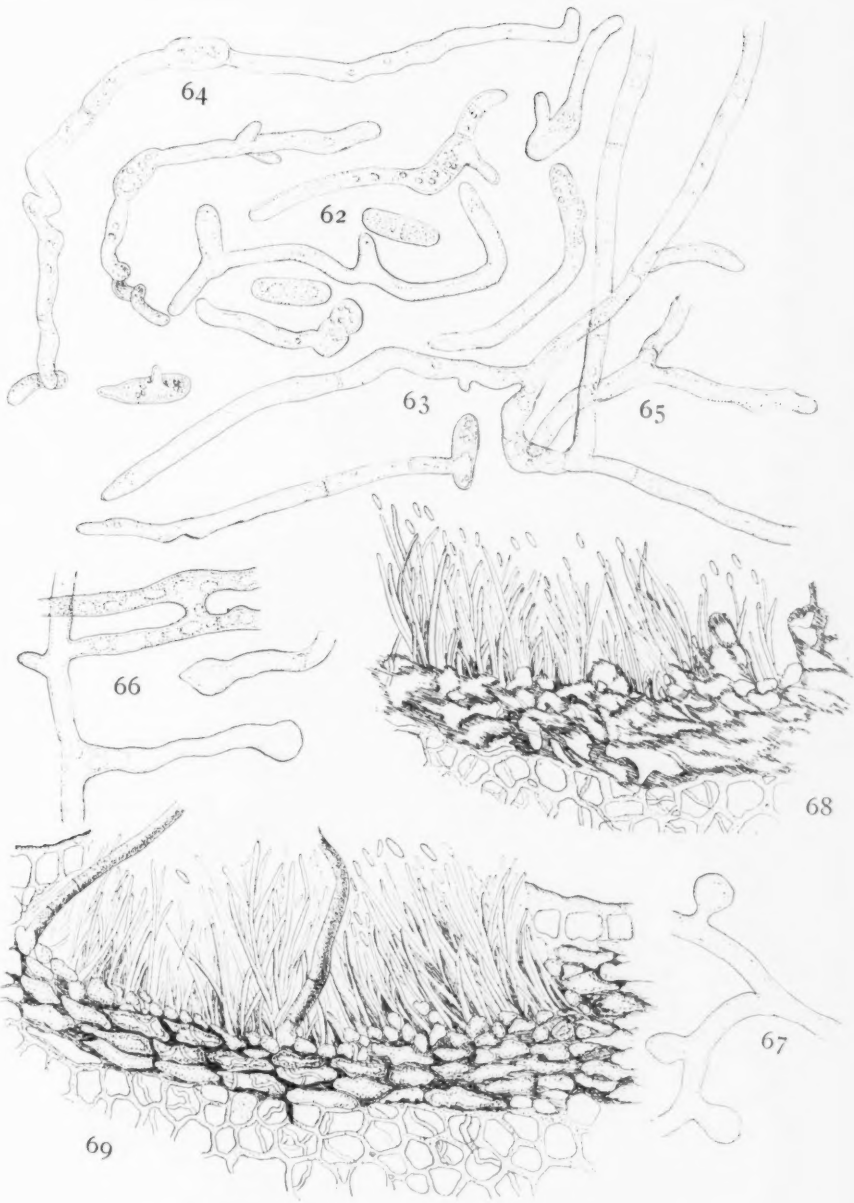

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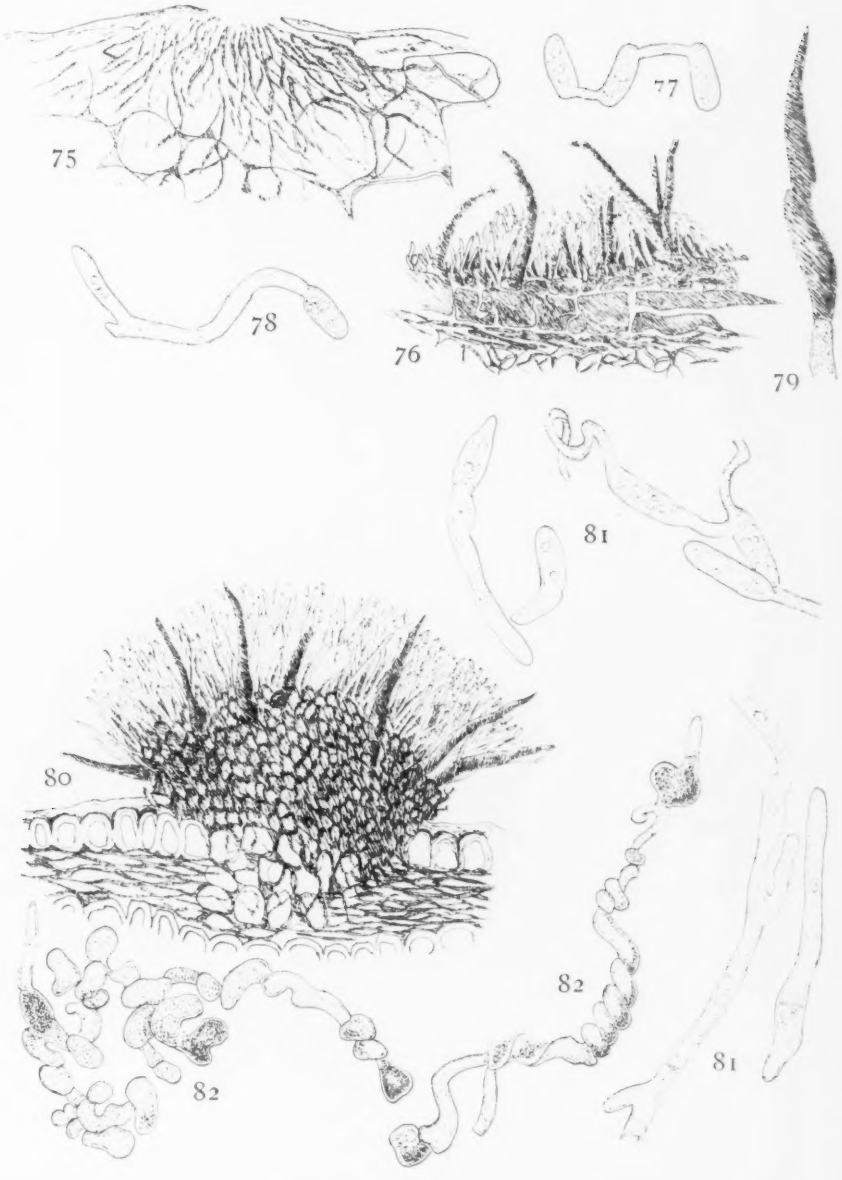

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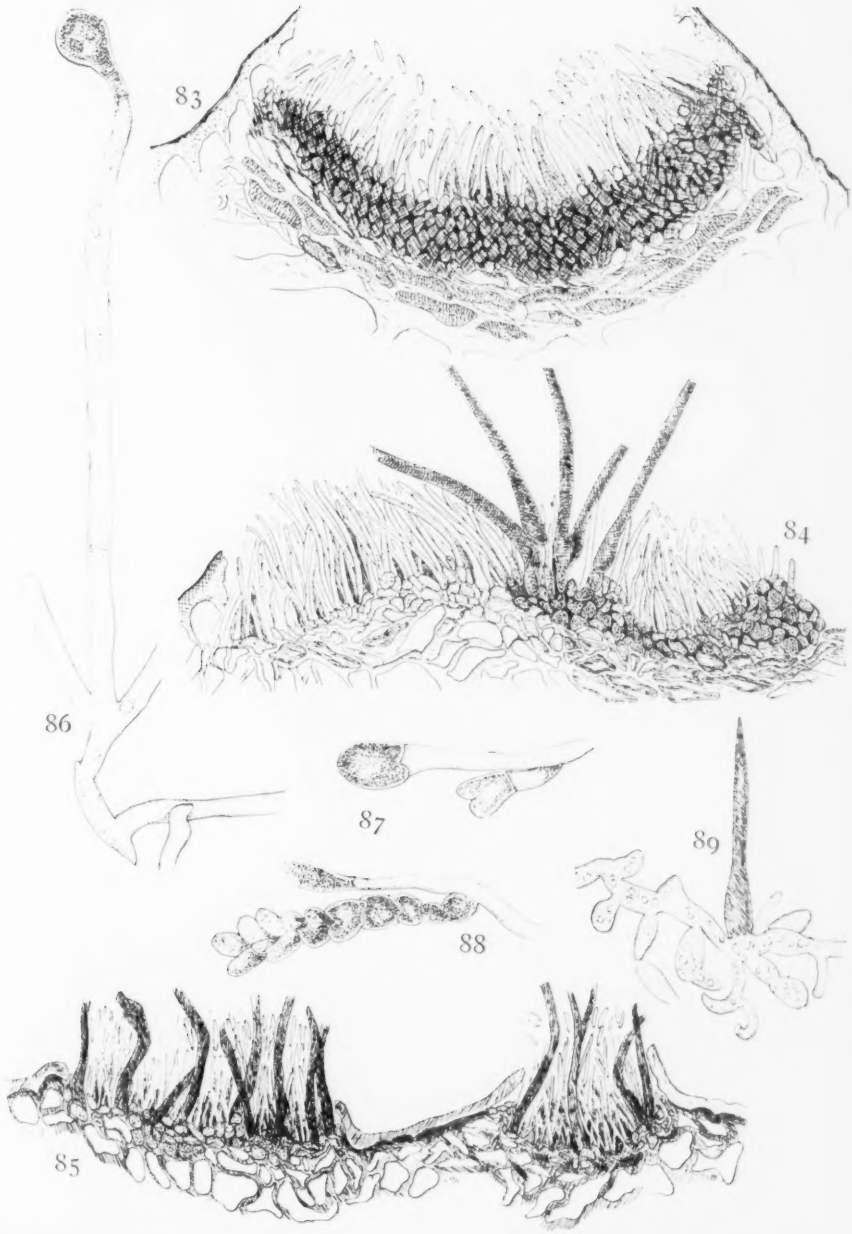

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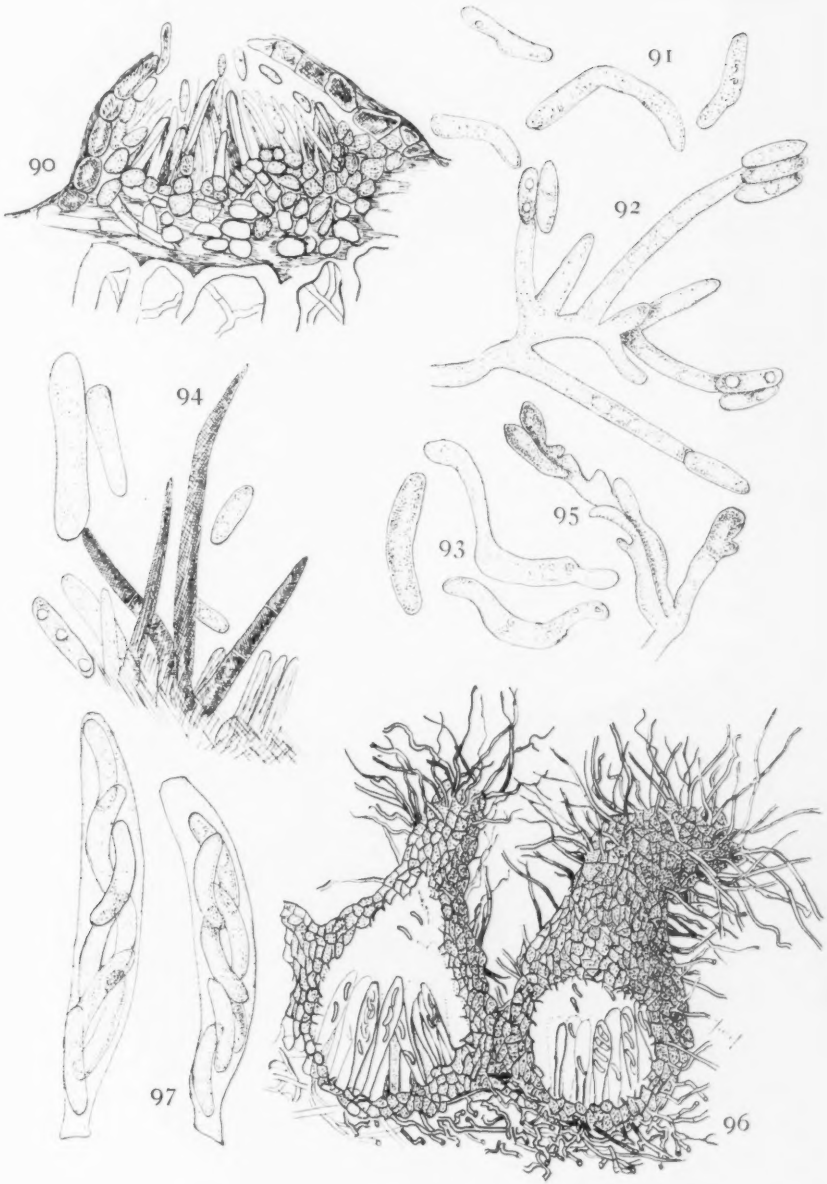

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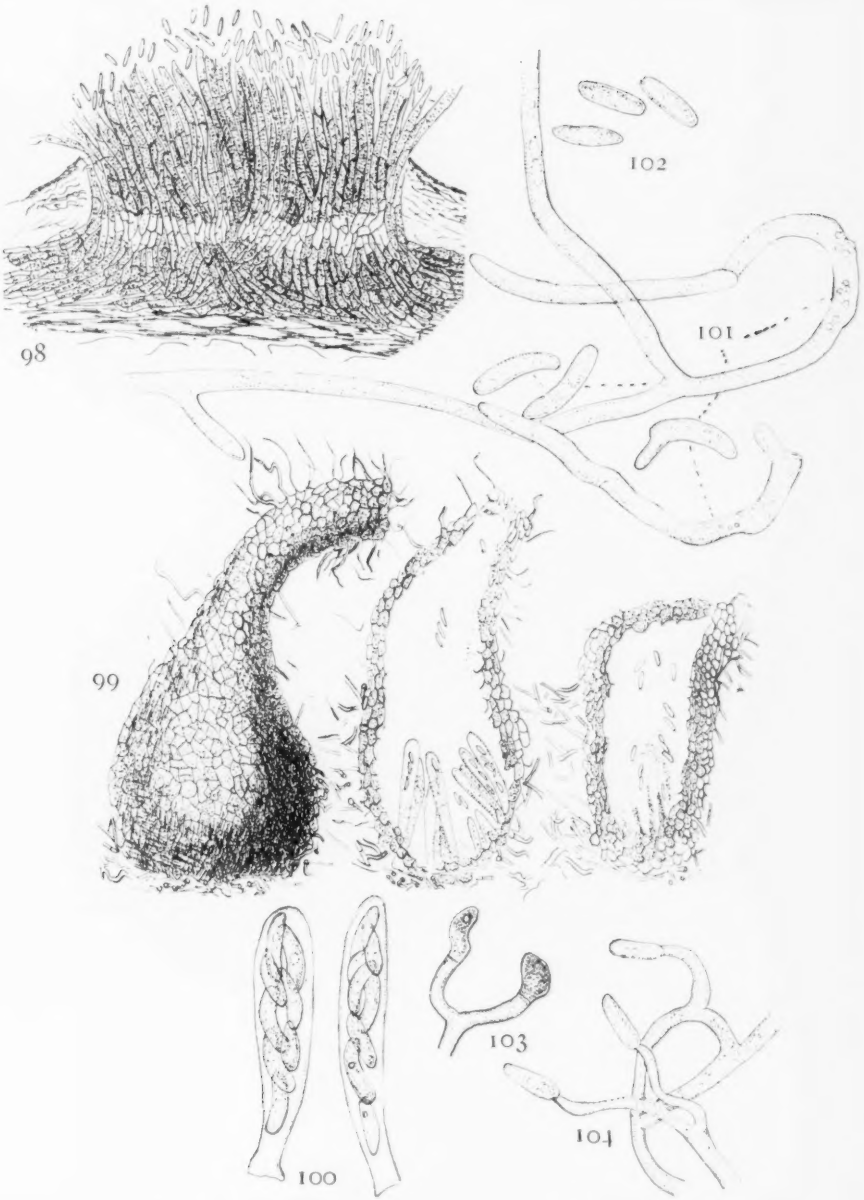

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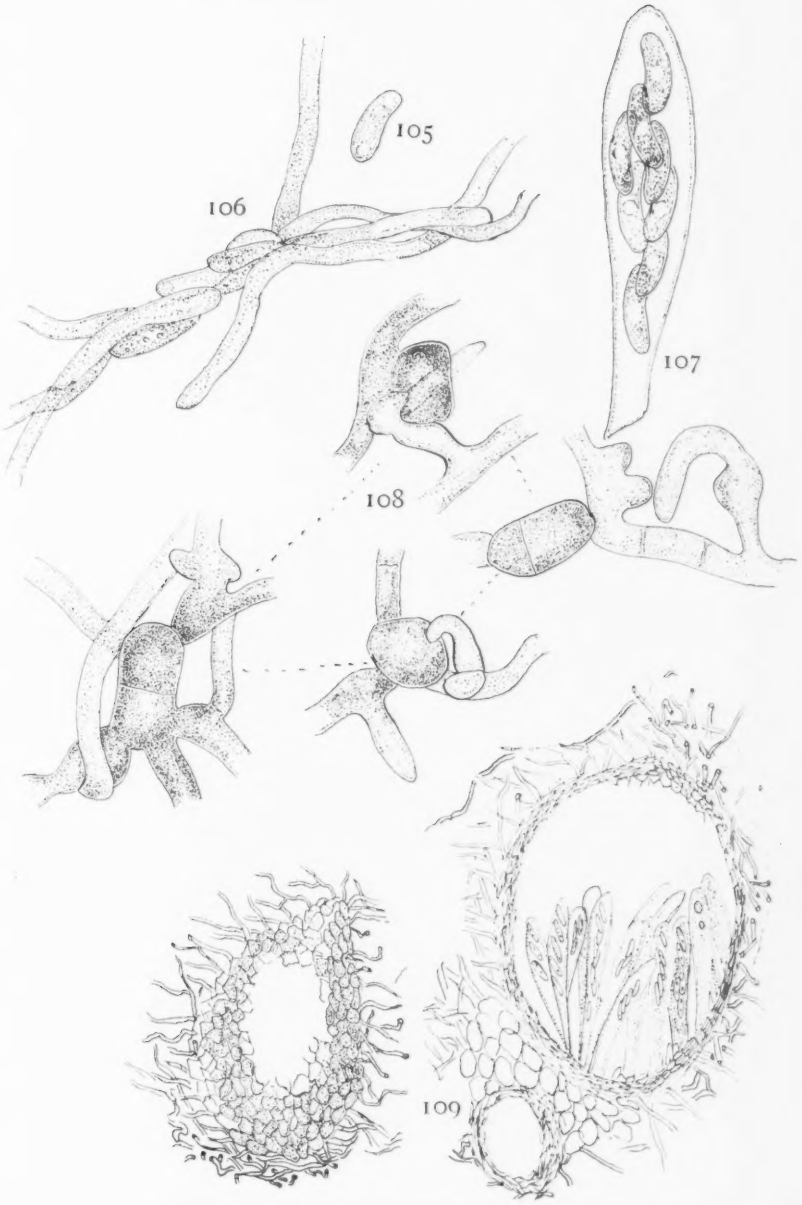

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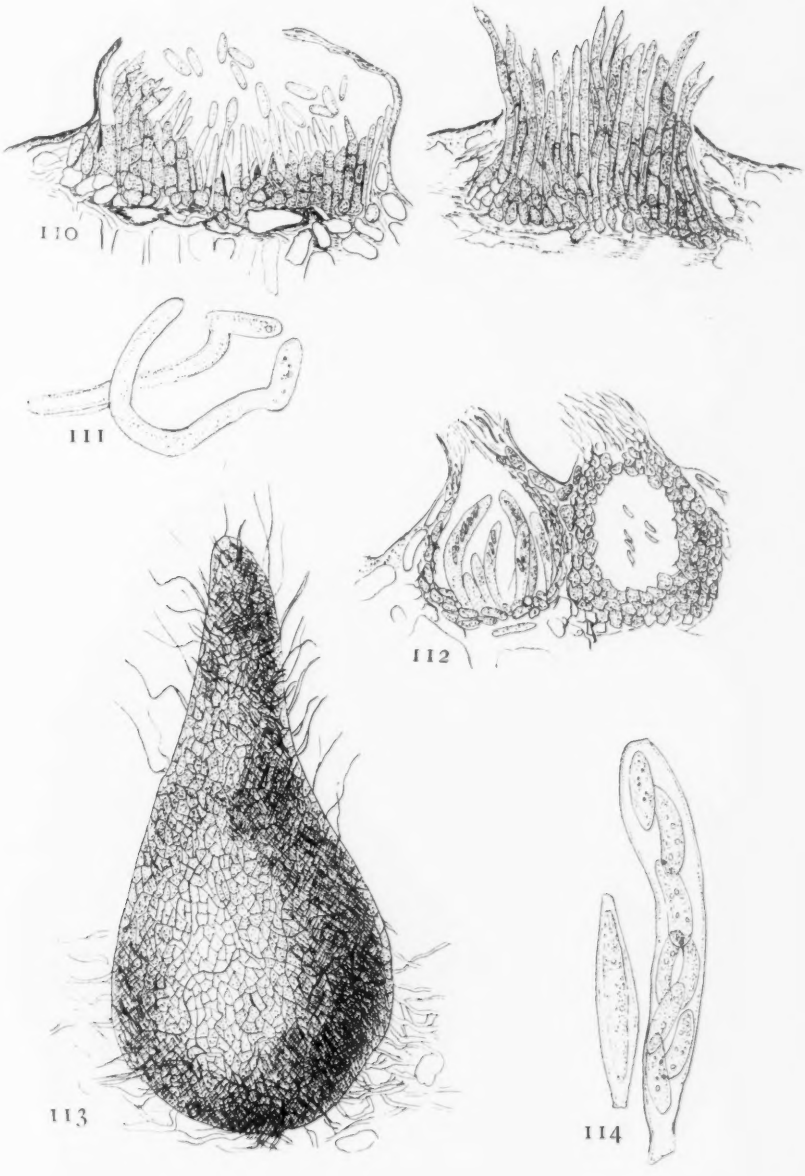

STONEMAN on ANTHRACNOSES

ON THE RELATION OF THE FLORA OF THE LOWER SONORAN ZONE IN NORTH AMERICA TO THE FLORA OF THE ARID ZONES OF CHILI AND ARGENTINE.*

WILLIAM L. BRAY.

THE relation of the flora of extra-tropical North America to that of extra-tropical South America was first discussed by Gray and Hooker in their report on "The vegetation of the Rocky mountain region and a comparison with that of other parts of the world,"[1] under the title "North American types in South America." In this report there was printed a list of some eighty genera which contained identical or more or less closely related species in the southwestern states and south of the equator, concerning which they remark:

> Clear if not very numerous indications exist that there has at some time been greater opportunity for extension of North American types into the southern hemisphere. It appears that this has taken place along the western side of the American continent, along the central part of North America and Mexico, and the western part of South America. When our cool temperate flora flourished only along or near the southern border of the United States, the warm temperate, to which most of the plants enumerated belong, was still farther south. When the climate became again warmer, a portion of these were as well placed for southward as for northward retreat.

Two years later Professor Engler[2] defined this relation of the two floras more precisely, presenting a revised list of about eighty genera, involving many species, characterized chiefly by the fact that they were elements of the Mexican plateau and

* For assistance in the preparation of this paper very cordial thanks are due to the management of the Berlin Herbarium, and in particular to Geheimrath Professor Adolph Engler, at whose suggestion the subject was taken up, and by whose friendly courtesy I was enabled to have free access to all of the resources of the herbarium.

[1] Bulletin U. S. Geol. and Geog. Surv. of the Territories **6**: —. 1880.

[2] Versuch einer Entwicklungs-geschichte der Pflanzenwelt **2**: 224. 1882.

portions of the bordering states, which, being mostly absent from south Mexico, Central America, and the Andes of Colombia, Venezuela, and Ecuador, reappear again first in Chili. Emphasis was laid upon the large percentage of Californian genera represented in Chili by identical or corresponding species, or even by species very distantly related, and their general absence in the intervening region.

These lists by no means included all the North American elements in Andean or extra-tropical South America, nor did they indicate that some very notable cases represented the extension of South American elements into extra-tropical North America, though of course these additional phenomena of distribution were discussed elsewhere in the *Entwicklungs-geschichte*, and it will be necessary to become familiar with them in the present paper.

More accurately defined the regions chiefly concerned are as follows:

1. In North America, the arid belt designated by Dr. Merriam[3] as the Lower Sonoran zone, including the Mexican tableland and adjacent western Texas, New Mexico, Arizona, Nevada, and Utah, with central, southern, and most of Lower California, approximately the region discussed by Professor Engler under "Das mexikanisches Hochland" and its northward extensions.

2. In South America, the desert of Atacama from about Cobija to 27° south and the less arid district south to 34°; the arid sand steppes and salt deserts of western Argentine along the east slope of the Andes, embracing in general from Catamarca at the north, Cordoba at the east, and Mendoza southward toward the Rio Colorado and Rio Negro; the "Chañar-Steppe" of Grisebach and "Monte Formation" of Lorentz.

With the above regions are also concerned the Gulf zone, with southern Brazil, Uruguay, and eastern Argentine; and the high Andes of Colombia, Venezuela, Ecuador, Peru, and Bolivia

[3] Geographical distribution of plants and animals, Year Book Dep. Agric. 1894: 207 (and note).

above 3000^{m}, in the latter of which a very prominent Mexican highland and boreal element occurs.

The vegetation with which we have here to deal is above all one of xerophytic stamp. It falls into the two following categories: (1) groups distributed more or less continuously along the continental axis, always interrupted by the moist tropical and subtropical belt from south Mexico to the Andes of Colombia and Venezuela (the subandine province of Engler[4]), but with a very marked development in the arid plains and plateaus of the two extra-tropical zones in question; (2) groups not at all high mountain plants, but existing both in the Chilian or Argentine arid zones and in the Lower Sonoran zone of North America, but entirely disconnected through the intervening distance. It is evident that group (2) will furnish the more interesting and difficult questions of distribution as related to genetic affinities. It is further evident that satisfactory discussion can follow only after a critical determination of what those affinities are. In the following pages the writer presents a great deal more than he has himself determined critically, recognizing also that some excellent illustrative groups are left unmentioned.

The instances cited from Amarantaceæ, Malvaceæ, Loasaceæ, and Leguminosæ are not the results of my own study, although I have been able to compare specimens in all of them. The Loasaceæ will be very fully treated in the forthcoming monograph by Drs. Urban and Gilg. Gomphrena, Malvastrum, Sphæralcea, and Prosopis deserve more special study in comparing the species of the different regions concerned. One of the very best illustrations was found in the Zygophyllaceæ, in which, of course, I have simply used the results of Professor Engler's study of the family. In the other cases I have made a rather more detailed study of the specimens in the Berlin Herbarium.

Amarantaceæ-Gomphreneæ.

This group of the Amarantaceæ is peculiarly the New World development of the family, finding there a subtropical and warm

[4] Entwicklungs-geschichte der Pflanzenwelt **2**: 206.

temperate habitat in both North and South America. The more pronounced xerophytic genera occupy the Lower Sonoran zone in North America, and similar portions of southern Brazil, Uruguay, Argentine, and in a few cases Chili, being connected through the gulf region rather than along the Andes. Certain of the genera, as Pfaffia, Iresine, and perhaps Alternanthera, are more nearly tropical, and prevail in the territory encircling the gulf of Mexico. Three genera, Cladothrix, Gossypianthus, and Dicraurus, are confined to the Lower Sonoran zone. Guilleminea extends from this zone along the Andes to Peru, *G. densa* having the distribution of the genus. Frœlichia has several distinct species in the two extra-tropical zones, with one, *F. Floridana*, generally distributed and perhaps in both.

Gomphrena affords the most noteworthy case of distribution. Of the ninety species, more than sixty are of extra-tropical South America, more than ten are Sonoran, and fifteen natives of Australia. *G. globosa* is the cosmopolitan member. It appears that the Australian species are quite as closely related to the South American as are those of the Lower Sonoran zone, and all three regions would indicate a distribution analogous to that I have shown in the case of the Frankenia § Toichogonia-Cosmopolita.[5]

In so far as special contrivances for distribution are present they are as follows:

1. The stems are jointed and fragile, and the flowers easily disarticulate from the rachis.

2. The perianth is beset with long woolly hair in most of the genera.

3. The perianth is furnished with stout barbed hairs (*Alternanthera repens*) or with setose or spiny excresences (Frœlichia).

4. The bracts are long and spiny tipped (Gomphrena, Alternanthera).

These characters would aid the fruit in adhering to hairy or woolly mammals.

[5] Geog.-Distr. of Frank. Engler's Botan. Jahrbücher **24** : 407.

MALVACEÆ.

Three genera, Sphæralcea, Malvastrum, and Sida, furnish good illustrations for our purpose. They are pronounced xerophytic genera, and have this noteworthy feature in common, that they occur in the Lower Sonoran zone, in the South American arid regions, and either in the Capland or in Australia.[6] In Malvastrum, while the type of the three regions (Sonoran zone, Argentine-Chili, etc., Capland) appears to be a common one, there occurs in the Andes of Chili and Peru the very distinct section Phyllanthophora described by Professor Schumann[7] as follows:

In Chili, und dem Andinen Gebiete überhaupt steigen die Arten der Gattung M. hoch in die Gebirge und nehmen einen durchaus alpinen Character an; sie sind durch niedrigen, dicht rasigen Wuchs mit rosettig gedrängten Grundbl. und starke graue Bekleidung ausgezeichnet. Diese Formen haben stets Bl., welche an den Tragblättern emporgehoben sind, und aus dem Stiele derselben hervorbrechen. Sie bilden die einzige wohl abgegrenzte Gruppe, die Asa Gray als Phyllanthophora bezeichnet hat.

In this connection the distribution of several species of Sida[8] is of interest, as follows:

Sida leprosa K. Schumann (*Malva leprosa* Ortega; *Sida hederacea* Torr.).—Uruguay, Patagonia, Argentine, Cuba, Mexico, Washington to southern California, Utah, Arizona, and W. Texas.

Sida hastata St. Hil. (*S. physocalyx* Gray).—Argentine, Uruguay, Mexico, Texas to Arizona.

Sida anomala St. Hil. (*S. fasciculata* T. & G.).—Matto Grosso, Uruguay, Argentine, Bolivia, Cuba, Florida, Texas, Mexico.

[6] Sphæralcea, four species in Capland; Malvastrum, fifteen species in Capland; Sida, seventeen species indigenous to Australia (see *Pflanzenfamilien* 3^6: —). Compare in this connection Gomphrena and Frankenia.

[7] Pflanzenfamilien 3^6: 41.

[8] This is being designated here the "Gulf zone distribution." Other illustrations are the following:

1. *Cienfugosia sulphurea* Garcke (*Fugosia Drummondii* Gray). Southwes, Texas, Mexico, southern Brazil, Paraguay.

2. *Spergularia Plattensis* Fenzl. Dallas, Texas, to southern California and south Brazil.

3. *Lepuropetalon spathulatum* Ell. Southern California, Georgia, Texas, Sonorat Chili, Uruguay, Montevideo.

4. *Polygala paludosa* St. Hil. Brazil, Paraguay, Louisiana, Texas.

The lack of mechanical devices for distribution in these genera seems not to have restricted them, which makes apparent the often substantiated fact that certain inherent ground gaining tendencies apparently render distribution independent of mechanical contrivances.

LOASACEÆ.

The Loasaceæ are almost exclusively a New World family, having, according to Gilg,[9] their center of distribution in Chili. The more extreme xerophytic genera spread thence over Argentine, and reaching North America find a second development chiefly in the Lower Sonoran zone. Four genera, Cevallia, Petalonyx, Eucnide, and Sympetaleia are endemic within this zone. Scyphanthus, Cajophora and Blumenbachia are southern extra-tropical. The largest genus, Loasa, furnishes many desert species for the Atacama and Argentine deserts, and while developed mostly in these regions and in the Andes, some species push north into Mexico (§ Saccatæ, 13 species, including *L. triphylla*, Peru to Mexico). But Mentzelia is the genus most conspicuous because of its distribution in the two zones under discussion, although quite abundantly distributed elsewhere, and particularly along the intervening Andes.

SEC. I. TRACHYPHYTUM, eight species; two Chili, one Chili-Argentine, one Argentine, four western North America, of which *M. albicaulis* reaches the plains and gulf coast.

SEC. II. MICROMENTZELIA, one species, *M. Torreyi*, in California and Nevada.

SEC. III. EUMENTZELIA, twenty-six species.

A. *M. aspera*, with the distribution of the genus; *M. oligosperma*, North American, east to Florida; two Argentine species.

B a. One Atacama, one California, one Florida, two Texas and north Mexico.

B b I α. Two Mexico, one Chili and Peru.

B b I β. Five Mexico, one Argentine.

B b II α. One Mexico.

B b II β. Two Mexico, one Bolivia, one Venezuela, one Colombia.

[9] Pflanzenfamilien 3^{6a}: 106. The above account of the Loasaceæ is taken from this source.

SEC. IV. DENDROMENTZELIA, one species, a large shrub or tree, Mexico.

SEC. V. BICUSPIDARIA, four Californian species, extending to Arizona and north Mexico.

SEC. VI. BARTONIA, six species.

A. Two species in western North America.

B a. One species in western North America.

B b. Three species; *M. albescens* in Argentine, Texas, and Mexico; two species in central and gulf states.

It appears from this synopsis, that although the development of the Loasacæ has proceeded in a manner to result in endemic genera in both the Sonoran zone and Chili-Argentine, still for Mentzelia, in particular, there is rather an intimate relation in distribution between the two regions.

The mechanical devices for distribution are such as to secure ready transportation by mammals or birds. The stems are exceedingly brittle, and all the younger parts are thoroughly beset with stout barbed pubescence, so that a very slight disturbance suffices to fasten the branch or capsule to the disturbing object.

LEGUMINOSÆ.

The Leguminosæ and also the Compositæ deserve special study in their distribution and relationships in the arid regions of North and South America. It suffices here simply to bring forward an illustration, and the genus selected is Prosopis, because in the remoteness of regions occupied and as a zonal genus it agrees with certain Zygophyllaceæ, *e. g.*, Larrea, Porlieria, and Bulnesia. Leaving out of account the two Asiatic and the two African species, there remain more than twenty New World species whose geographical center is in Argentine. These fall into two sections:

ALGAROBIA. Nineteen species, mostly in Argentine, but including the noteworthy *P. juliflora*, the mesquite, which in its distribution has come to occupy all of the subtropical and warm temperate, more or less arid districts of the western hemisphere. Apparently the Lower Sonoran zone would be very accurately

defined by the North American distribution of *P. juliflora*, and its occurrence in the Andes, the West Indies, etc., marks those zones which enter secondarily into the discussion of distribution between extra-tropical North and South America.[10]

STROMBOCARPA. Six species; *P. torquata*, *P. strombulifera*, and *P. reptans* in Argentine; *P. heterophylla*, *P. cinerascens*, and *P. pubescens* in the more arid portions of the Lower Sonoran zone (west Texas, Mexico, and westward). Of *P. pubescens* Dr. Merriam[11] says:

> This mesquite, commonly known as "screw bean," is widely distributed over the deserts of the southwest, usually in company with the preceding (*P. juliflora*).

While the Sonoran and Argentine species of Prosopis are more nearly related than the wide geographical separation would seem to allow, only in the case of *P. juliflora* does there seem to have been ready interchange between the regions.

The genus is favored for a wide distribution by reason of the sugary mesocarp, which makes an article of food for herbivorous animals, the hard indigestible seed being in this way carried in the alimentary canal uninjured, and left with excrement in favorable situations for germination. This is more especially the case in § Algarobia, and above all in *P. juliflora*, of which Dr. Havard[12] says:

> The ripe pod or "bean" contains more than half its weight of assimilative nutritive principles, and is therefore a valuable article of food. The most important of these is sugar, in the proportion of 25 to 30 per cent. Most herbivorous animals, but especially the horse and mule, are fond of this pod and thrive on it. In the field it is a welcome though imperfect substitute for grain. The mesquit "bean" is one of the staple foods of Mexicans and Indians.

These facts would seem sufficient to insure a very general distribution. That the Strombocarpa species are not wanting in

[10] Compare Bulnesia and Heterostachys.

[11] Shrubs of the Death Valley Exped. North Amer. Fauna **7**: 300.

[12] Report on flora of S. and W. Texas. Proc. U. S. Nat. Mus. **8**: 498.

[13] Op. cit. 499.

a similar quality is shown by the following, also from Dr. Havard:[13]

> The twisted pod or bean contains a spongy and nutritious pulp, rich in sugar, and is used as food by the Mexicans and Indians.

POLYGONACEÆ-ERIOGONEÆ.

This group of the Polygonaceæ, embracing eleven genera, is notably characteristic of southern California and the adjacent arid regions. Kœnigia is an exception, being an arctic and subarctic species. Of the remaining ten genera, six are confined to southern and Lower California and adjacent islands. Eriogonum, by far the largest genus, is distributed over the whole of western United States, although its chief center of development is also California. Lastarriæa has one species found in both California and Chili. Oxytheca has five Californian species, of which one is in Chili. Chorizanthe embraces some twenty-five Californian species (Euchorizanthe), of which one is in Chili; while there is a peculiarly Chilian group, Chorizanthopsis, of about ten species, none of which are in California.

Southern California appears clearly the center of development of Polygonaceæ-Eriogoneæ, and the Chilian representatives, therefore, may be referred to this region for their immediate or more or less remote origin.

Lastarriæa Chilensis, although described as a Chilian plant, is evidently Californian originally. It possesses a very wide distribution in the coast and hill country of Chili, likewise throughout southern California. The plants of the two regions are so nearly identical that a very recent distribution must be supposed. This has probably occurred in connection with the shipping of stock, particularly of sheep, as the plant is especially adapted for such means of distribution (1) by the recurved hooks of the involucre, and (2) by the easy breaking off of the younger parts of the stems.

Oxytheca dendroidea Nutt. falls in the same category as *L. Chilensis* Remy; and the same may be said of *Chorizanthe com-*

missuralis Remy, which, being one of the Euchorizanthes of California, occurs in Chili without noticeable variation. All of these species are fitted especially for distribution by cattle or sheep; but by whatever means they have come to Chili, it is safe to infer (1) that they are Californian, and (2) that this distribution has occurred in very recent times.

But comparing Chorizanthopsis with Euchorizanthe, the case is fundamentally different. Any intimate connection between these sections must be referred to an age long past. This is shown by the totally different methods by which they have adapted themselves to xerophytic conditions. The Californian species are all short-lived annuals, adapted for growing in the very driest places. The whole time of growth, flowering, and maturing seed lasts but a few weeks. With the approach of rainless parching weather their work is completed.

Of the Chilian species, all are shrubby, and often in sandy places form dense patches as a means of mutual protection. They are wholly different in habit from the Californian species, and are the one exception in Polygonaceæ-Eriogoneæ where stipules are produced. This section would appear to be an offshoot from Euchorizanthe, as Oxytheca and Eriogonum are, although the change is not, as in those, within the involucre, but in the vegetative structure. In its shrubbiness Eriogonum is very similar to subgenus Chorizanthopsis. The same circumstances which witnessed the rise and spread of Eriogonum over western North America may have witnessed also a more general distribution of the group into the southern hemisphere, of which the Chilian Chorizanthes are the remnant.

It is interesting to note in connection with this group that several genera which have special devices for distribution are narrowly endemic. Pterostegia and Harfordia have the bracts developed into bladder-like structure, for wind distribution; Centrostegia has wing-like, spurred involucral bracts; Nemacaulis and Hollisteria have woolly involucral bracts and perianth; while Phyllogonum has neither bracts nor involucre. All of these are limited to southern California and adjacent

islands. Kœnigia, which has no special mechanism for distribution, is the most widely distributed of all.

FRANKENIACEÆ.[14]

The Frankeniaceæ are typically halophytic plants, represented in the new world as follows:

FRANKENIA § TOICHOGONIA-COSMOPOLITA, six species in Chili on the coast and in the alkali regions inland. Of these *F. grandifolia* is abundant on the California coast, about salt lakes of southern California, and eastward to southern Arizona, New Mexico and northern Mexico, the inland type being var. *campestris* Gray.

F. § TOICHOGONIA-ISOLATA, three species: *F. farinosa*, about Cobija in northern part of desert of Atacama; *F. triandra*, the Puna region, at 3500 to 4000^{m}; *F. vidali*, islands of San Felix and San Ambrosio, Chili.

F. § BASIGONIA, two species: *F. Palmeri*, Lower California to San Diego bay; *F. Jamesii*, east foot of Rocky mountains in Colorado and western Texas.

NIEDERLEINIA: *N. juniperoides*, salt steppes of Argentine; nearly related to *Frankenia* § *Basigonia*.

The Frankeniaceæ illustrate two features in the relation between the two regions of North and South America now under discussion.

1. That a very recent distribution has taken place in the case of *F. grandifolia*, which belongs to a section notable for the number of closely related species. This distribution may be due to birds, since the plant is found so widely distributed inland and at a considerable height above the sea (1000^{m}).

2. That *F. Palmeri*, *F. Jamesii*, *F. triandra*, and others, and *Niederleinia juniperoides* are isolated species, which we may regard as remnants of a previously widespread development; and therefore no interchange between the regions occupied has occurred under present geological conditions.

CHENOPODIACEÆ.

The Chenopodiaceæ should be considered in this connection,

[14] For detailed discussion of the geographical distribution of the Frankeniaceæ see Engler's Jahrb. **24**: 394. 1897.

notwithstanding the fact that there are many cosmopolitan species. A very useful instance is furnished by the genus Spirostachys, of which *S. occidentalis* is the North American form, occurring throughout the salt steppes of the Lower Sonoran zone; and *S. vaginata* and *S. Patagonica*, two nearly related South American species from the Argentine salt steppes, where they are abundant and conspicuous. I am inclined to believe there is no recent connection between the species of these two regions. *Heterostachys Ritteriana* merits mention here, because, aside from Spirostachys, the other nearly related genera are in the central Asiatic salt steppes and Australia; and the plant further illustrates the phenomenon of Gulf zone and southern Brazil distribution, being described from Central America, northern South America, the West Indies, southern Brazil, and Argentine.[15]

ZYGOPHYLLACEÆ.

The critical work done by Professor Engler on this family[16] makes it of special value for our purpose. He has shown that there is a very considerable development of the Zygophyllaceæ in the New World, of which the larger portion form the consistent group Guajacineæ, which is the present expression of a branching off from Old World Zygophyllaceæ in geological times. With few exceptions the Zygophyllaceæ in the western hemisphere are limited to the Lower Sonoran zone in North America and its corresponding zone in Argentine and Chili. The regions in addition are savannas of Venezuela and Colombia, southern Florida, West Indies, and southern Brazil; exactly the previously mentioned Gulf zone distribution.[17] Following is a tabular arrangement of the Zygophyllaceæ, based upon Professor Engler's study of the family:

[15] See under Malvaceæ.

[16] Pflanzenfamilien 3^4:74; Geog. Verbr. der Zygoph. im Verh. zu Syst. Glied. Abh. Kön. Preuss. Acad. Wiss. zu Berlin, 1896.

[17] Compare Prosopis, Heterostachys, and references under Malvaceæ.

	Sonoran zone, North America	W. Indies, S. Brazil, northern S. America	Chili-Argentine xerophytic zone	Means of distribution
1. Fagonia *cretica*	var. *Californica;* San Diego, Los Angeles bay, N. Mex. (val de las Palmas)		var. *Chilensis;* N. Chili (Coquimbo, Tarapaca, Atacama, etc.). var. *aspera;* Quebrada de Gaihuano.	Mucilaginous seed coat with spirally coiled projectile hairs, fitted for adhering when moistened.
2. Guajacum	*G. parvifolium;* Mexico. *G. Coulteri;* Mexico.	*G. officinale;* Fla,, Antilles, Guiana, Venez., Colombia (arid coasts). *G. sanctum;* Fla., Bahamas, Antilles, Guatemala.		Thin fleshy exocarp which birds would eat.
3. Porlieria	*P. angustifolia;* Texas, Mexico.		*P. hygrometrica;* N. Chili, Peru. *P. Lorenzii;* Argentine steppes.	
4. Pintoa			*P. Chilensis;* N. Chili.	No special mechanical device for distribution.
5. Bulnesia		*B. arborea;* a high tree in savannas of Col. and Venez.	*B. bonariensis;* Santiago del Estero; west slope of Sierra de Cordoba. *B. Schickendantzii;* Catamarca. *B. Chilensis;* Atacama. *B. foliosa;* Catamarca. *B. macrocarpa;* dune sand, campos of Catamarca. *B. Sarmientii;* Gran Chaco, Argent.	Broad winged fruit, adapted for distribution in open, arid steppes.

	Sonoran zone, North America	W. Indies, S. Brazil, northern S. America	Chili-Argentine xerophytic zone	Means of distribution
6. Plectrocarpa			*P. tetracantha*; salt regions from Catamarca to Mendoza.	Carpels with curved spines.
7. Larrea	*L. Mexicana.*		*L. divaricata*; covers exclusively great areas of Cordoba and Mendoza.	Carpels with long, thick-walled hairs.
			L. cuneifolia; salt deserts, Cordoba to Rio Colorado.	
			L. nitida; Argentine.	
8. Metharme			*M. lanata*; Tarapaca, N. E. Chili.	
9. Tribulus *terrestris*	In both hemispheres xerophytic in warm temperate zones.			Carpels tuberculate, or rough spiny in some cases, which would aid in transportation by mammals. Compare Malvas of a similarly wide distribution, which have no mechanical device for transportation.
	T. Californicus; S. Ariz., Lower Calif.			
	T. brachystylis; N. Mex.; Guaymas, Mexico.			
10. Kallistrœmia			*K. tribuloides*; Brazil and Argentine.	
	K. maxima; Texas, N. Mex.	*K. maxima*; Bolivian Andes northward through Central America and West Indies		
	K. grandiflora, Texas to Calif.			

	Sonoran zone, North America	W. Indies, S. Brazil, northern S. America	Chili-Argentine xerophytic zone	Means of distribution
11. Viscainoa	*V. gemmulata*: Lower Calif.			Fruit of four splitting capsules, not winged, still light enough to be carried by winds.
12. Chitonia	*C. Mexicana*; Montezuma river.			Fruits large and winged, splitting at maturity.
13. Sericodes	*S. Greggii*; N. Mexico.			Woolly carpels.
14. Peganum	*P. Mexicanum*; N. Mexico; nearly related to Chinese species.			Like Fagonia.

The distribution of *Fagonia cretica* vars., Tribulus, and Kallistrœmia is similar to that of *Frankenia grandifolia*, *Chorizanthe commissuralis*, *Oxytheca dendroidea*, *Lastarriæa Chilensis*, etc.; that of Larrea and Porlieria is like the isolated Frankenias, Spirostachys, etc. Larrea may be cited as the best case illustrating that phase of distribution in which there is absolute separation of the species both in a geographical and a genetic way. No other species are more reliable determinants of zonal areas that those of Larrea;[18] which is also to say that distribution from one zone to another over thousands of miles in which Larrea could not grow is very improbable, and this is clearly indicated by the distinctness of the species. Professor Engler expresses the opinion[19] that the present condition of Larrea, and indeed of the Guajacineæ,

[18] MERRIAM, North American Fauna 7: 293; Engler, Pflanzenfamilien 3^4: 86.

[19] Geogr. Verbr. der Zygophyllaceæ, etc. Abh. Preuss. Akad. Wiss. —: 17. 1896.

represents remaining parts of a prehistoric, more general development, *e. g.*:

> Nun haben wir bei Larrea die eigenthümliche Verbreitungserscheinung, das *L. Mexicana* Moric. vom Colorado-Gebiet Californiens, bis zum westlichen Texas und im trockneren Mexiko verbreitet ist, während drei andere Arten in den Sandsteppen und Salzwüsten Argentenien von den Anden bis Cordoba in ausgedehnten Beständen auftreten. Diese Arten sind sowohl von einander, wie auch von der mexikanischen sehr verschieden, so dass die Entstehung dieser Arten sehr alten Datums sein und eine grössere Anzahl von ausgestorbenen Arten angenommen werden muss, welche sowohl morphologische wie räumlich de jetzt lebenden Larrea-Arten mehr verknüpften.

REVIEW OF HALOPHYTIC ELEMENTS.

Following is a tabulation of halophytic species occurring beyond the tropics in North and South America. Certain endemic species of Suæda and Atriplex are believed not to be related through the cosmopolitan coast species. In no other genus, except Prosopis, are species known to occur in the intervening distance, *i. e.*, over 40° of latitude:

Lower Sonoran halophytic	Chili-Argentine halophytic
Spirostachys occidentalis.	Spirostachys { vaginata; Argentine. Patagonica; "
Suæda; *e. g.* S. Torreyana and S. suffruticosa	Suæda; *e. g.* S. divaricata.
Atriplex; *e. g.* A. canescens.	Atriplex; *e. g.* A. Chilense (Chili) (*cf.* A. cinereum; Austral.)
Frankenia grandifolia, - - =	F. § Toichogonia-cosmopolita; Chili.
F. Jamesii, F. Palmeri, related to	Neiderleinia juniperoides; Argentine.
Fagonia cretica Californica.	Fagonia cretica { Chilensis; Chili. aspera; Chili.
Larrea Mexicana.	Larrea divaricata; Argentine.
	" nitida; "
	" cuneifolia "
	Metharme lanata; Chili.
Prosopis § Algarobia; P. juliflora.	Prosopis § Algarobia; P. juliflora and many others, mostly Argentine.
§ Strombocarpa, 3 species.	§ Strombocarpa, 3 species; Argentine.

In the above will be noted (1) the greater number of common genera in Argentine and the Lower Sonoran zone; (2) that most species have no special mechanical devices for seed transportation.

Borraginoideæ-Eritrichieæ.

The Borraginoideæ-Eritrichieæ of the *Pflanzenfamilien* include seventeen genera, of which two, Lappula and Eritrichium, possess a broad distribution in the temperate zone of both hemispheres. Seven genera are chiefly E. Asiatic. Eight other genera occur in western North America, of which four recur in Chili. The geographical center of this group would appear to have been eastern Asia. From here the migration would have been along the chain of islands, Aleutian, etc., joining Asia and America, or by Behring strait and along the continental axis to extra-tropical South America; and hence the group would fall in with the boreal element represented in the Andes of Bolivia, Peru, and Chili. But the group has attained a distinct development in the Lower Sonoran zone of North America, and in the Atacama-Chilian arid zone, and for that reason is discussed here in some detail. It is to be noted that at one time or another, almost all of the west American development of Borraginoideæ-Eritrichieæ (both north and south) has been referred to the genus Eritrichium (excepting, of course, Amsinckia), and this fact may be made important in interpreting the present condition of the group in the western hemisphere. The Eritrichium type still prevails in a few species, and these are notable for being high mountain forms distributed along the continental axis from Alaska to southern Chili, with a considerable interruption from southern Mexico to Ecuador, while the forms referred to distinct genera represent apparently the variations resulting from the occupancy of a vast arid tract.

In the *Synoptical Flora* (191–199, ed. 1), Asa Gray included all of North American Borraginoideæ-Eritrichieæ under Eritrichium, Echidiocarya, and Amsinckia. In *Proc. Amer. Acad.* **20**: 264, and *Syn. Fl.* Suppl. 423–433 (ed. 2), the two latter are retained,

while Eritrichium in North America practically disappears in Krynitzkia and Plagiobothrys. Later, Professor Greene[20] defines the following genera: Allocarya, Eremocarya, Piptocalyx, Sonnea, Plagiobothrys (incl. Echidiocarya), Oreocarya, Cryptanthe, and Amsinckia. This is the arrangement adopted in the *Pflanzenfamilien*. Professor A. Philippi[21] describes one hundred Chilian species in twelve groups under Eritrichium, besides recognizing Amsinckia and Plagiobothrys. The one hundred species of Eritrichium fall under Allocarya, Eremocarya (?), and Cryptanthe.

In the following tabulation species are grouped under those characters which best emphasize the relation of the Chilian to the North American species:

	Western N. America	Chili
1. Cotyledons two-lobed AMSINCKIA. (boreal species.)	A. echinata A. intermedia } =	A. angustifolia.
2. Nutlets rugose, depressed from above; scar in middle of concave ventral face; lower leaves opposite. ALLOCARYA.	A. stricta A. trachycarpa } =	(E.) uliginosum.
	A. chorisiana A. plebeia } =	(E.) procumbens. (E.) humilis. (E.) sessifolium.
3. Nutlets very strong, thick, depressed (as in 1), very broad; stipe in middle of ventral face. PLAGIOBOTHRYS.	P. rufescens = ((E.) fulvum.)	P. rufescens. ((E.) tinctorium?)
4. Nutlets united in pairs to an elongated stipe-like base. ECHIDIOCARYA.	E. Arizonica.	None.

[20] Pittonia, pts. 1, 2, 3. 1887.

[21] Plantæ Nuevas-Chilensis, 1893.

	Western N. America	Chili
5. Nutlets with rugosity prolonged into barbed spines.	Two species.	None.
6. Nutlets with very thin, often crustaceous or pearly dotted or tubercled pericarp attached to gynobase along the whole grooved ventral face, or at base by triangular area; fitting together by plane faces. CRYPTANTHE. EREMOCARYA.	Many species.	Many species.
(1). Nutlets unlike or only one or two maturing: calyx articulated with and easily falling from rachis.	Cryptanthe angustifolia. C. crassipetala.	(E.) aspera. (E.) Bridgesii. (E.) congesta. (E.) carrizalensis. (E.) minutiflora. (E.) glareosa.
(2). Four nutlets maturing: not of extreme xerophytic habit.	Many North American species of Cryptanthe.	(E.) chætocalyx. (E.) debilis? (E.) axillare?
More xerophytic.	Eremocarya micrantha.	(Eritrichium) parviflora.
(3). Nutlets very large, protruding beyond calyx; pericarp crustaceous, silvery white.	Cryptanthe Jamesii.	(E.) gnaphalioides, and most amphicarpous species.
(4). Calyx circumscissile.	In several groups.	None.
(5). Calyx lobes with long, foliose tips, mostly thickly beset with long, needle-like hairs: more extremely xerophytic.	C. Torreyana. C. leiocarpum. C. intermedium. C. ambigua. C. barbigera.	(E.) longiseta. (E.) micrantha. (E.) calycina. (E.) diffusum. (E.) diplotrichium.
(6). Species with amphicarpous nutlets.	None.	Fourteen species.

The foregoing synopsis of characters does not always bring together plants of similar habit, as, for example, *Cryptanthe Jamesii* (N. America) and *C.* (*Eritrich.*) *gnaphalioides* (Chili), but it does aid in showing (1) that the Chilian species are an expansion of the North American development, and (2) that while identical species exist in the two zones there was also possible a distribution long enough ago to permit noticeable individuality to arise in the Chilian group.

To summarize briefly: More than 130 species of Borraginoideæ-Eritrichieæ have been described in western North America, of which over 60 per cent. are confined to the Sonoran zone. Fewer than ten of these species pass into northern Mexico; but one into southern Mexico. In the Chilian xerophytic zone, from 23° S. to 34° S., more than one hundred Borraginoideæ-Eritrichieæ have been described, of which five or six are high mountain forms of a wider distribution southward and northward, especially in the high Andes of Peru, Bolivia, and Ecuador. But there remains a region of more than twenty degrees latitude from which Borraginoideæ-Eritrichieæ are absent, or in which they occur very sparingly.

The southward extension of this group may be ascribed in part to glacial agency, inasmuch as some species belong to the high Andean boreal element. Mechanical arrangements for distribution are found in the easy disarticulation of the fruit, and its needle-like hairiness in Cryptanthe and Eremocarya; in the roughened or spined carpels of certain species; and in the long, sharp-haired calyx lobes of others.

With the Borraginoideæ-Eritrichieæ may be presented also the genus Pectocarya. The genus embraces the two sections Ktenospermum and Gruvelia.

KTENOSPERMUM has the same species, *P. linearis*, in California, Utah, Arizona, and in Chili. From California north to British Columbia is var. *penicillata*, and in Peru a similar var. *lateriflora*.

GRUVELIA has *P. setosa*, a distinctly marked species confined to southern California and Nevada. There is a more common and widely distributed form of this section which Gray added to

the Chilian *P.* (GRUVELIA) *pusilla*. It is not identical with *P. pusilla*, and to call it a variety of that species hides the essential fact that the Chilian plant is a southward migration of the common form of GRUVELIA.

The flat light carpels of Pectocarya are admirably adapted for clinging to birds or mammals because of the pectinate margin with its recurved setæ.

POLEMONIACEÆ.

The Polemoniaceæ duplicate the characteristics of the Borraginoideæ-Eritrichieæ in being a boreal group with a marked development in the Lower Sonoran zone of North America, repeated in a less marked degree in the Chilian zone. Except for the genus Gilia the family would scarcely come within the scope of this discussion, being in their South American distribution high mountain species.

Gilia includes some eighty North American species, falling under thirteen sections; and about fifteen Chilian species, mostly included in Eugilia, Navarretia, and Dactylophyllum, but, as in Cryptanthe, having an individuality of species that indicates a prehistoric as well as modern distribution.

Western N. America	Chili
§ EUGILIA.	*Gilia laciniata*, described originally from S. Amer.; occurs likewise in western N. Amer.
Gilia multicaulis, western California, is of *G. laciniata* type; straggling laciniate-leaved forms doubtless=	*G. laciniata.*
Gilia capitata and *Gilia achillæfolia* are more extreme California and Oregon species, related to - -	*G. laciniata.*
Gilia inconspicua, Wyoming to western borders of Texas, and west to California and British Columbia; forms with laciniate radical leaves very close to - - - -	*G. crassifolia.* *G. copiapina.* *G. longifolia.*

Western N. Amerfca	Chili
	Gilia fœtida, distinct Chilian species. *Gilia glabrata* and *G. ramosissima* are Chilian species of common Eugilia type.
§ NAVARRETIA.	
Gilia intertexta, plains of Columbia river to California and the Rocky mountains - - - - =	*G. involucrata* (incl. *G. Navarretia* Steud., and *G. eryngioides* Lehm.).
Gilia minima, of arid portions of interior of Oregon and Nevada to Colorado and Dakota - - =	dwarf forms of *G. involucrata* in Chili.
§ DACTYLOPHYLLUM.	
Gilia pusilla, Guadaloupe island, and var. *Californica*, Sacramento to Nevada, - - - - - =	*G. pusilla*, in Chili.
COLLOMIA.	
Collomia linearis Nutt., Saskatchawan, Oregon, Washington, and Utah, - - - - - =	*Collomia coccinea* Lehm., Peru, Bolivia and Chili.
Collomia grandiflora Dougl., similar to preceding, plains from Rocky mountains to California and Nevada.	
Collomia gracilis, Alaska to Chili.	
POLEMONIUM.	
Polemonium micranthum - - =	*P. antarcticum*.

In the preceding tabulation the more extreme xerophytic species do not appear, because it is only the mountain species which have the extended distribution, and among which, therefore, the same or closely related species occur in both Chili and western North America. The method of distribution is of interest here. Commonly in the Polemoniaceæ the seed is furnished with a layer of cells whose walls become mucilaginous by contact with water, expelling forcibly the spirally thickened hair-like processes which cause the seed to adhere firmly to moistened

objects (*e. g.*, feet of birds) and thus secure transportation. So far as I was able to examine, all the South American species of Polemoniaceæ possess these mucilaginous seeds. *Gilia minima* and dwarf forms of *G. involucrata* (Chili) grow in little dense mats in arid spots. On the addition of moisture the seeds are gradually pushed up from the dense enclosure of bracts until they stand exposed and ready to adhere to any disturbing object. In the section Navarretia the bract development itself would be sufficient to bring about extended distribution by clinging to the hair of mammals. The absence of these genera from both north and south Mexico is noteworthy.

Summary.

1. Most of the genera just considered are of pronounced xerophytic or halophytic character.

2. Characteristic American groups, such as Zygophyllaceæ, Guajacineæ, Borrag.-Eritrichieæ, Amarant.-Gomphreneæ, and Loasaceæ, tend to a development in both extra-tropical xerophytic zones, often with the same, and generally with nearly related species in both zones.

3. For some genera each zone has its characteristic group of endemic species, indicating an independence from the other reaching into prehistoric time, *e. g.*, Malvastrum, Chorizanthe, Larrea, etc.

4. The halophytic genera in particular indicate that in some cases no distribution has occurred from one region to the other under present geological conditions, *e. g.*, *Frankenia Palmeri*, *F. Jamesii*, *F. triandra*, *Niederleinia juniperoides*, Spirostachys, Larrea, etc.

It is evident from a study of the plants concerned that distribution by natural methods has occurred and is occurring under present physical conditions. It is further evident that distribution has been greatly facilitated by what may be called, in contradistinction, artificial means, namely, as a result of commerce.

Again, one must suppose the present conditions, or others as favorable, to have endured far back into the history of the pres-

ent plant world to allow time enough for the isolation of such groups as Chorizanthopsis, Malvastrum § Phyllanthophora, or even for the Chilian development of Borrag.-Eritrichieæ.

But how does it occur that the high andean flora is chiefly boreal? And how have the arctic-alpine plants reached the southern high Andes from the Rocky mountains? Further, how have the sharply defined and isolated species of Larrea, Frankenia, Prosopis, etc., come to be in both regions?

Gray and Hooker supposed that in the glacial time there was a driving of boreal and warm temperate elements southward, as a result of which some plants were placed favorably for migration farther south. Engler suggests that the southward migration of animals caused by the glacial encroachment was very notable in aiding the distribution of plants southward over the isthmus.

It has been suggested that geological conditions have allowed a more general extension along the west American coast of an arid plateau similar to that of middle and northern Chili. Referring to a chart of ocean depths along the Pacific coast it is clear that by an uplift of 3000 feet a series of abrupt step-offs or shelves would be exposed extending to the Californian coast, and making the isthmus region a broad belt of land. This, besides offering a highway for xerophytic elements, would also bring about that union of the Pacific islands off the Californian coast with the continent which Sereno Watson[22] supposed must have prevailed in order to give the similarity of island flora to that of California. He suggested that the relations to the adjacent continent indicate a former flora which spread over a wide region now submerged, from which ancient flora the elements common to California and Chili were derived.

Such a condition of emergence along the west coast would be very favorable as an explanation for many of the phenomena of distribution, but I am not convinced that it is either necessary or possible to assume this. One must bear in mind that an elevation of the coast of South America by 3000 feet would in all

[22] On the flora of Guadaloupe islands. Proc. Amer. Acad. 11: 112. 1876.

likelihood mean an elevation of the Andes much higher above their present summits than we are warranted in ascribing to them. Professor Engler[23] says that the Andes of Venezuela, Colombia, and Ecuador could not have been completely glaciated during the glacial period, for in this zone we find peculiar tropical genera which, without doubt, date from the oldest times. In this event these mountains could not, within the era of present vegetation (dating presumably from somewhere in the Tertiary period) have had a much greater elevation than at present. On the other hand, there is conclusive evidence of a state of submergence during the Tertiary period and of subsequent upheaval, a fact significant in the present discussion. He says[24] in effect: If the geological conclusions be correct, we have in the Tertiary period the Andes representing an island separated from the Guiana-Brazilian triangle of land by an arm of the sea, narrow at the north, wider at the south, and from Central America by a strait. Central America was united with western North America, which latter was separated from eastern North America by inland seas. In these conditions an exchange of tropical elements between Central America, West Indies, Guiana-Brazil, and the Andes could occur. With the progress of upheaval of the Andes and consequent changes of climatic conditions the tropical nature of these mountains was modified, only those forms remaining which could adapt themselves to the extremes of greater altitude. With this elevation, in particular, the flora of the north pushed southward over a newly opened territory, peopling the Andes in such numbers that the present high andean vegetation is to be reckoned with the boreal. This southward wandering of North American species was at first of the hygrophilous elements, embracing many forms coming from the Himalayas to North America, and so explains the presence of Himalayan types in the Andes. But, as the Andes began to attain their present elevation, the moisture of the trade winds was withdrawn, and a pathway for more xerophytic elements was

[23] Entwicklungsgeschichte der Pflanzenwelt 1: 198.

[24] ENGLER: Entwicklungsgeschichte 1: 196–198.

opened, and so the xerophytic hosts, which had previously found favorable territory for expansion and variation in western North America, pressed southward; for example the Sonoran Compositæ, Polemoniaceæ, Cactaceæ, Borragineæ, etc. These, by the agency of birds and mammals, were carried over the equator to the extra-tropical regions of Chili, where again they found a broad, open territory favorable to a varied development.

Three important propositions result from the foregoing:

1. We are carried back to a time when the isolated groups, like § Chorizanthopsis and Malvastrum § Phyllanthophora could have branched off from the North American stem.

2. Conditions following the appearance of land along the eastern base of the Andes might account for a more general distribution of those genera like Frankenia, Niederleinia, Larrea, and other Zygophyllaceæ, Spirostachys, and some other Chenopodiaceæ, which are now widely separated and genetically distinct.

3. Animals, particularly birds and mammals, have probably played a prominent part in the distribution of plants across the equatorial and isthmus regions.

In the following tabulation the devices for securing distribution are brought together for a general view:

I. Adaptation for wind distribution:
   1. By winged fruits: Bulnesia, Chitonia, Centrostegia, Pterostegia, Harfordia.
   2. By light, woolly hairs: Larrea.

II. Adaptation for distribution by animals.
   1. Probably by birds.
      (*a*) As food; fleshy exocarp: Guajacum, Porlieria.
      (*b*) Seeds with mucilaginous covering and elastic coiled slime hairs: Gilia, Collomia, Fagonia, Peganum.
      (*c*) Seeds very small; without special devices for clinging, yet possibly adhering to birds' feet in mud or slime: Frankenia, Spirostachys.
   2. Probably by mammals.
      (*a*) As food; nutritious mesocarp: Prosopis.
      (*b*) By devices for clinging to wool or hair.

(1) Involucral bracts with recurved hooks; stems fragile at joints: Chorizanthe, Oxytheca, Lastarriæa.
(2) The whole plant beset with barbed hairs; stems very brittle: Loasaceæ.
(3) Rough or spiny projections on calyx or carpels: Tribulus, Kallistrœmia, some Cryptanthes, Frœlichia.
(4) Calyx with sharp, sometimes recurved stiff hairs; fruits easily falling away; many Borrag.- Eritrichieæ.
(5) Carpels flat, with hooked setæ: Pectocarya.
(6) Fruits adhering by woolly covering: Gossypianthus, Frœlichia, Gomphrena.

For most species, then, the distribution and relationships in the two zones are such as can be accounted for from data that are reasonably well established. The element which remains rests upon very much the same basis of speculation as the relation of New World to Old World Zygophyllaceæ, or Australian and South American Chenopodiaceæ, or, indeed, the relation of the great salt desert regions of the world to each other.

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CURRENT LITERATURE.

NOTES FOR STUDENTS.

ALFRED J. EWART[1] continues to hold it as proved, in spite of Kny's objections, that isolated chlorophlastids may continue to assimilate for a short time after removal from the parent cell.—J. M. C.

IN HIS INTRODUCTORY presentatation of the pteridophytes, Sadebeck[2] outlines five main groups, FILICALES, SPHENOPHYLLALES, EQUISETALES, LYCOPODIALES, and CYCADOFILICES. The three groups of FILICALES are *Fil. leptosporangiatæ* (with the natural isosporous and heterosporous subdivisions), *Marattiales*, and *Ophioglossales*. The EQUISETALES are subdivided, on the basis of isospory and heterospory, into *Euequisetales* and *Calamariales*. The LYCOPODIALES have as their main divisions *Lyc. eligulatæ* and *Lyc. ligulatæ;* the subdivisions of the former being *Psilotineæ* and *Lycopodiineæ;* of the latter, *Selaginellineæ*, *Lepidophytineæ*, and *Isoetineæ*. The taxonomist who delights in uniformity of group names, and also names that indicate the rank of groups, will not be pleased.—J. M. C.

THE INTERESTING discovery of a set of the plants collected on the Lewis and Clark expedition and named by Pursh forms the subject of a paper by Mr. Thomas Meehan.[3] Pursh in his *Flora* refers to 119 as having been collected, many of which were new. The fate of the collection was unknown, the general understanding being that Pursh took the plants to England, and left them to Lambert, an officer of the Linnean Society, and that upon the distribution of Lambert's herbarium the plants were scattered. The occurrence of a large number of types in the collection made the loss of it a serious one. It seems that two years ago Professor C. S. Sargent suggested to Mr. Meehan that some of the material might be in the custody of the American Philosophical Society. After a long search the original packages were found unopened, some of them in bad condition, but the collection as a whole fairly preserved. Pursh's labels and notes made the discovery certain. The collection was sent to the Gray Herbarium for final identification, and Mr. Meehan includes in his account the very full and satisfactory report by Dr. B. L. Robinson and Mr. J. M. Greenman. Several interesting discoveries were made which will correct certain current identifications. In presenting the report parallel columns are used, one giving the present name of the plant, the other the treatment of the plant in Pursh's *Flora*. The discovery

[1] Bot. Centralbl. **75**: 33–36. 1898.

[2] Engler and Prantl's "Die Natürlichen Pflanzenfamilien" 1[4]: 1–48. 1898.

[3] Proc. Acad. Nat. Sci. Philad. 12–49. 1898.

of this important collection of North American plants and its deposit in the Academy of Sciences of Philadelphia is a matter of congratulation among taxonomists.—J. M. C.

MR. HENRY H. DIXON[4] has published recently some very interesting papers upon transpiration, which deal with the results of experiments which satisfy the author that transpiration is a "vital" process rather than a physical one. By "vital" processes he means "those which cannot be accounted for by the immediate energy-relations of the organism to the external world, but those in which energy previously stored by the organism, *e. g.*, oxidizable materials, is utilized, and which only take place during the life of the organism." During transpiration, therefore, the elevation of water in the vessels resembles the raising of water in plants by root pressure. The phenomena of transpiration responded sufficiently to oxygen and to anæsthetics to suggest that it is connected with vital phenomena. The conclusions drawn from experiments in a saturated atmosphere are as follows:

1. The elevation of the water of the transpiration current, when the leaves are surrounded with a saturated atmosphere, is effected by pumping actions proceeding in the living cells of the leaves.

2. The observations on the drying back of branches furnished with dead leaves renders it highly probable that these vital pumping actions are partially or wholly responsible for the elevation of water even in an unsaturated atmosphere.

3. These pumping actions are capable of raising the water against an external hydrostatic pressure.

4. In common with other vital actions, they are accelerated by a moderately high temperature, and are dependent on the supply of oxygen.

5. The cells adjoining the terminal portions of the water conduits appear to possess this activity, and, in plants provided with water-glands, the pumping actions are not limited to the secreting tissues of these glands.—J. M. C.

THE GENETIC RELATIONSHIPS between the phanerogams and cryptogams in the light of the most recent investigations are discussed by Belajeff.[5] As the title would indicate, the paper presents no new facts. Little attention is paid to the sporophyte, but the evolution of the male and female gametophyte, from the bryophytes to the spermatophytes, is presented in a masterly way. The female gametophyte shows a gradual transition from independence in the bryophytes to complete dependence in the gymnosperms and angiosperms, and the archegonia which it bears show a gradual transition from forms with the neck and venter free to forms with the entire archego-

[4] On the effects of stimulative and anæsthetic gases on transpiration, Proc. Roy. Irish Acad. III. **4**: 618–626. 1898; Transpiration into a saturated atmosphere, *l. c.* 627–635.

[5] Biol. Centralbl. **18**: 209–218. 1898.

nium imbedded. The homologies of the embryo sac structures of the angiosperms are not yet cleared up.

Up to 1885 there is nothing in literature to justify the assumption of such a gradual transition in case of the male gametophyte. Belajeff investigated antheridia of Selaginella and Isoetes in 1885, and the antheridia of the heterosporous Filicineæ in 1890. The small cell cut off from the germinating spore of Selaginella and Isoetes is the male gametophyte, the homologue of the prothallium which bears the antheridia in the homosporous Filicineæ. The antheridium which this much reduced gametophyte bears consists of several peripheral cells forming a wall enclosing inner cells in which spermatozoids are formed. The peripheral cells later coalesce. In the heterosporous Filicineæ the more complex male gametophyte shows that the transition from cryptogams to phanerogams is not to be sought here but rather in the heterosporous lycopods.

In the gymnosperms Belajeff investigated only the conifers. In the Abietineæ the small cells cut off from the germinating microspore represent the male gametophyte. The rest of the spore consists of an inner small cell surrounded by a large outer cell which develops the pollen tube. The inner cell divides into two, the hindmost of which disorganizes; the other again divides, giving rise to two cells which are the homologues of the mother cells of the antheridia of Selaginella and Isoetes. In the Cupressineæ the male gametophyte is entirely suppressed, the pollen grain transforming itself directly into an antheridium. In the Taxineæ the simplification is carried still further.

In the angiosperms the conditions are the same as in the Cupressineæ, the pollen grain dividing into two cells, the larger representing the antheridium wall, which stretches into a tube, the smaller dividing into two generative cells.

In 1897 the studies of Ikeno and Hirase threw new light upon the relationships of the cryptogams and phanerogams. Hirase found that the two generative cells in the pollen tube of Gingko develop into ciliated spermatozoids, and Ikeno made the same discovery in Cycas. Webber recently made similar observations on Zamia, his description of the development of the spermatozoids corresponding with Belajeff's description of these structures in Equisetum and ferns, thus adding another proof of the relationship between the cryptogams and cycads. Of course these observations break down the old division into zoidiogams and siphonogams, since Cycas, Gingko, and Zamia would belong to both groups. — CHAS. J. CHAMBERLAIN.

ITEMS OF TAXONOMIC INTEREST are as follows: Recent numbers of the *Bulletin of the Torrey Botanical Club* contain descriptions of new species of Asclepias and a recasting of *A. verticillata* and its allies, by Anna Murray Vail (**25**: 171–182. 1898); some new species of liverworts, with two plates, by Marshall A. Howe (*l. c.* 183–192); descriptions of various new species

from the west, with three plates, by A. A. Heller (*l. c.* 193–201, 265–271); descriptions of various new Wyoming plants, with plate, by Aven Nelson (*l. c.* 202–206, 275–284, 373–381); a revision of the N. Am. Eurhynchia, by A. J. Grout (*l. c.* 221–256), in which *Cirriphyllum* is proposed as a new genus including the species (four) with the concave filiform-tipped leaves, *Bryhnia* Kawin recognized to include two species with papillose leaves, and *Eurhynchium* retained to include the remaining nine species, one of which is new; miscellaneous new plants from New Mexico, by E. O. Wooton (*l. c.* 257–264, 304–310); miscellaneous new plants, by John K. Small (*l. c.* 316–320); about three dozen new fungi, by Chas. H. Peck (*l. c.* 321–328, 368–372); a presentation of the genus *Syntherisma* (often called the Digitaria section of Panicum) in North America, by George V. Nash (*l. c.* 289–303), twelve species being recognized, two of which are new, and most of the others with new combinations.—M. L. Fernald (*Proc. Boston Soc. Nat. Hist.* **28**: 237–249. 1898) has been studying the much discussed genus Antennaria and presents a synopsis of the New England species, all included in our manuals under the "polymorphous" *A. plantaginifolia*, recognizing thirteen species and varieties. The same author (*Erythea* **6**: 41–51. 1898) has also attacked the species complex known as *Castilleia parviflora*, and recognizes fourteen species and varieties, eleven of which are new.—C. V. Piper (*Erythea* **6**: 29–32. 1898) has recently described some miscellaneous new species from Washington.—B. L. Robinson (*Proc. Am. Acad.* **33**: 305–334. 1898) has published revisions of Mimosa and Neptunia. The North American and Mexican species of Mimosa are presented, sixty-seven being recognized, nine of which are new. A new subgenus, ASTATANDRA, is established to include *M. tequilana* Wats. Four North American species of Neptunia are recognized, one of which is new.— J. M. Greenman (*Proc. Amer. Acad.* **33**: 455–470. 1898) has published revisions of Galium and Relbunium, so far as species of Mexico and Central America are concerned. Twenty-five species of Galium are included as belonging to the region, five of which are new. Relbunium, included by Dr. Gray in Galium, includes seven species, one of which is new. The same author (*l. c.* 471–489) has also described numerous miscellaneous new and critical species from Mexico. —W. Willard Ashe (*Jour. Elisha Mitchell Sci. Soc.* **14**: 51–54. 1898) has described a new Robinia (*R. Boyntonii*) from the southern Alleghanies. —E. L. Greene (*Pittonia* **3**: 313–328. 1898) has recently described six more new species of Viola, five new forms of Antennaria, six new species of Convolvulus, and reëstablishes Rafinesque's *Polycodium*, including the *stamineum* group of Vaccinium (six species), and Nuttall's *Batodendron*, with *V. arboreum* as a type and two new species.— Dr. A. Weber continues his publications on Cactaceæ (*Bull. du Mus. d'hist. nat.* 1898; nos. 2 and 3), dealing with the genus Echinocactus in Lower California, and with Pereskia and the Pereskia-like opuntias of Mexico.—J. M. C.

NEWS.

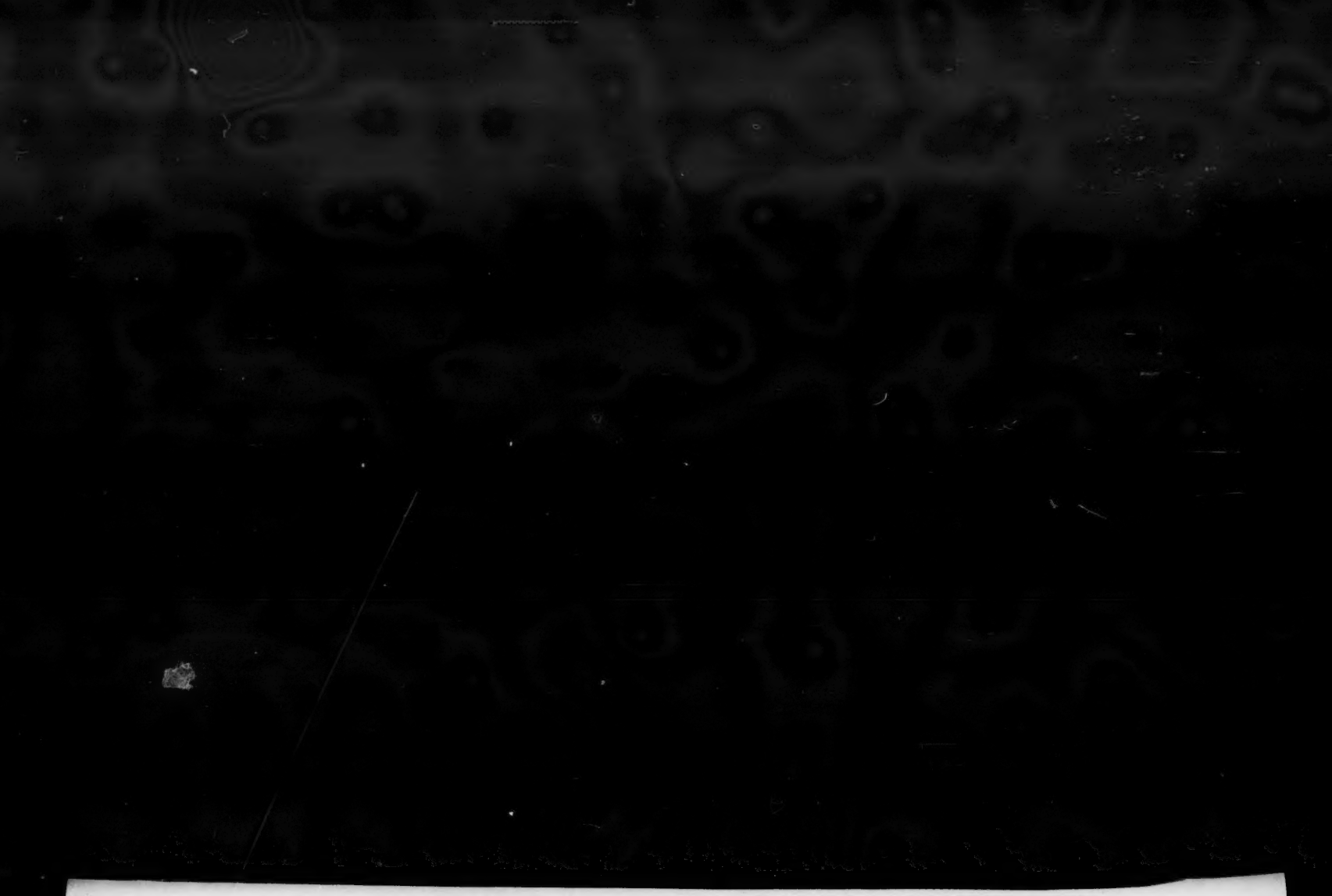
PROFESSOR W. W. BAILEY, after twenty-one years of continuous service at Brown University, has been granted leave of absence for the first term of 1898–9.

ILLUSTRATIONS of the inflorescence and dissections of Welwitschia (Tumboa), made from a plant growing at Kew, are published in the *Gardener's Chronicle* (III. **24**: 62–63. 1898).

THE DIVISION OF BOTANY of the Department of Agriculture has issued a bulletin (no. 20), prepared by V. K. Chestnut, which describes and illustrates the principal poisonous plants of the United States.

MR. JOHN W. HARSHBERGER has published his lecture upon the uses of plants among the ancient Peruvians. Among the prehistoric remains are found the maize, peanut, potato, sweet potato, and coca.

THE LAST FOUR NUMBERS (171–174) of Engler and Prantl's *Natürlichen Pflanzenfamilien* contain a continuation of the Umbelliferæ, by Drude; a continuation of the Hymenomycetineæ, by Hennings; and the beginning of the Pteridophyta, by Sadebeck.

THE BERLIN ACADEMY OF SCIENCE has made the following grants for botanical work: 2000 marks to Professor Engler for the continuation of his work on East African plants; 600 marks to Professor Graebner, for the continuation of his work on German heaths; 500 marks to Dr. Loesner, for the completion of his monograph of the Aquifoliaceæ.

DURING THE LAST COLLEGE YEAR the following botanists have passed their doctorate examinations at the University of Chicago: W. L. Bray, thesis "The xerophytic flora of Texas;" Otis W. Caldwell, thesis "Morphology of *Lemna minor*, with ecological notes;" Henry C. Cowles, thesis "The ecological relations of the sand dune flora of northern Indiana;" W. D. Merrell, thesis "Contribution to the life history of Silphium."